University of Alberta

Life history patterns of male white-faced capuchins (*Cebus capucinus*): Male-bonding and the evolution of multimale groups

By

Katharine Mary Jack

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Anthropology

Edmonton, Alberta

Spring 2001

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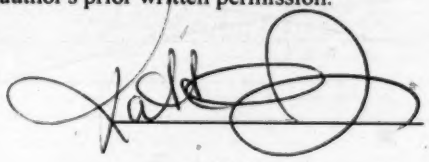

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Life history patterns of male white-faced capuchins (Cebus capucinus): Male-bonding and the evolution of multimale groups*, submitted by *Katharine Jack* in partial fulfillment of the requirements for the degree of *Doctor of Philosophy*.

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Date April 11/07

DEDICATION

To Craig

for your love, encouragement,

and ability to make me laugh no matter what.

To Mom and Dad

for encouraging me to be the person I have become.

ABSTRACT OF THE DISSERTATION

Male cooperation in competition with outsiders (male-bonding) has been suggested to occur more easily between related males. Such cooperative aggression has been observed among coresident male white-faced capuchins (*Cebus capucinus*); a species characterized by male dispersal and female philopatry and group males are presumed unrelated. In this study I address the question of why males cooperate by examining male dispersal patterns, affiliative relationships, and the effect of male emigration on the vigilance behavior of coresident males. During a 15 month field-study, 1430.75 hours of focal data and additional *ad libitum* data were collected on all males over 4 years of age (N=15) in four groups of white-faced capuchins in Santa Rosa National Park, Costa Rica. I also make use of the behavioral and demographic data collected on these monkeys since 1984.

Male natal emigration in white-faced capuchins appears to occur in response to an attraction to extragroup males or dispersing coresident males, while secondary emigration results from an attraction to extragroup mates. Once males reach adulthood they change groups approximately every four years and parallel dispersal (i.e. dispersing with group mates or into groups containing familiar males) remains high even during secondary migrations. Parallel dispersal enables males to retain familiar allies during group transfers and appears to influence male relationships within groups. The number of months males have resided together was a significant factor in predicting male affiliative relationships within groups. Group size was also significantly associated with affiliative interactions among coresident males; i.e. males residing in small groups were more affiliative than male residing in larger groups.

The effect of male emigration on the vigilance of coresident males indicated that additional males within groups confer both costs and benefits. Costs relate to an increased amount of time devoted to monitoring the social environment when additional coresident males are present. Benefits relate to the finding that some males are able to devote less time to non-social vigilance (vigilance for predators and conspecifics) when additional males are present in the group.

However, the vigilance behavior of males, particularly non-social vigilance, is highly variable and influenced by multiple factors (e.g. season).

ACKNOWLEDGEMENTS

Financial support for this project came from the National Geographic Society (Grant 6332-98), Natural Sciences and Engineering Research Council of Canada (NSERC post-graduate scholarship), Alberta Heritage Scholarship fund (Ralph Steinhauer Award), Ruggles-Gates fund for Biological Anthropology (Royal Anthropological Institute), Sigma-Xi, the Faculty of Graduate Studies and Research/Department of Anthropology at the University of Alberta, and an on-going operating grant from NSERC to Linda Fedigan. Additional support during the initial period of research design and grant writing was provided by a University of Alberta Faculty of Graduate Studies and Research Ph.D. Scholarship. The writing stage of this dissertation was supported by an Izaak Walton Killam Memorial Scholarship from the University of Alberta.

I thank the Area de Conservación Guanacaste, in particular Roger Blanco, for permission to conduct research in Santa Rosa. I am also grateful to my advisor and mentor Linda Fedigan for allowing me to observe her long-term study groups, and for her enduring support and assistance throughout this project. I would also like to thank the many students and researchers who have helped collect the life history data on the Santa Rosa white-faced capuchins since 1984. Without your hard work much of this project would not have been possible. I am grateful to Joan Silk for sharing her FOCOBS data entry program with a long line of capuchin researchers. The production of this dissertation was improved through discussions, editorial, and/or statistical advice from Linda Fedigan, Lisa Hansen, Craig Lamarsh, Mary Pavelka, Susan Perry, Jens Roland, Tracy Wyman, and Sandra Zohar. Thanks are also extended to several anonymous reviewers for their comments and suggestions on chapters four and five. I also would like to thank my committee members Pam Asquith, Mary Pavelka, Jens Roland, Karen Strier, and Pam Willoughby. Thanks also to Owen Beattie for chairing my defense.

Special thanks go to my field assistants, Dale Morris and Sasha Gilmore, not only for the hundreds of hours they spent following the capuchins through the forest and recording their every move, but for their friendship and the fantastic memories that go along with it. I cannot think of

either of you without smiling. The many researchers and fellow albergue residents in Santa Rosa also deserve a world of thanks: Barb Welker, Katie MacKinnon, Martin Dohrn, Tanya Smith, Jamie Cabrera, Nico Reyes, Graeme Hunt, Sarah Carnegie, Jon Sullivan, and Laura Molles. Good friends were made; thank you all for helping me keep my sanity, or perhaps losing it, while in the field. The cries of "have fun" as I trudged out to the forest at 4:30 am were especially appreciated. Alex Perez provided invaluable assistance with trail maintenance, water pressure, and antenna troubles; muchas gracias por su ayuda mi amigo. I also thank Alejandro Masis; friend, merengue partner, chauffeur, and excursion organizer. Thanks for getting us all out of the park once in a while. My thanks are also extended to the many people at ACG for answering my endless questions and helping me with field logistics: Roger Blanco, Maria Martha, Germo, Xiomara, and Magda.

To Brenda Simons, a good friend who doesn't talk about cows; thanks for keeping me company during my many months of writing. I am also grateful to my family: the Jacks, Lamarshes, and Rainbows. You have all supported my endeavors and encouraged me to follow my dreams. Profound thanks to Craig Lamarsh: best friend, field assistant, ever patient and loving husband. I am also eternally grateful to our two amazing dogs. Thanks Jasper, a.k.a. Doodle Bug, for keeping my feet warm while I spent the long winter writing. Eddie, I appreciate your unconditional love, constant watch, and unending energy; you got me out of the house when I needed it most. Finally, I thank all of the white-faced capuchins who let me steal a glimpse of their fascinating lives.

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CHAPTER ONE

Introduction

OVERVIEW OF DISSERTATION

Male-bonding, or the formation of cooperative bonds among group living males, particularly during group defense against conspecifics, has been suggested to occur more easily among related males and, therefore, to be most pronounced in species characterized by female dispersal and male philopatry. Similar male-bonding has, however, been observed in white-faced capuchins (*Cebus capucinus*); a species in which males emigrate from their natal group prior to physical maturity and in which the adult males of a group have been presumed to be unrelated. In white-faced capuchins, the cooperation of males appears to be necessary to enter into a group and to prevent outsiders from taking over. Male takeovers have been observed in this species and the resultant interactions among males are often violent with severe (and sometimes fatal) wounding occurring. Such takeovers have resulted in the eviction of resident males, infanticide, and the deaths or disappearances of both males and females. But why would these presumably unrelated males, residing together and competing for mates and resources, cooperate with one another? How are males benefiting by tolerating the presence of others in their group?

In this study I address these questions of male-bonding in white-faced capuchins by examining male dispersal patterns (both natal and secondary), the effect of male emigration on the vigilance behavior of coresident males, and the affiliative relationships among males within groups. During the continuous 15 month field study, my assistants and I collected 1430.75 hours of focal data, and additional *ad libitum* data, on 15 male white-faced capuchin monkeys residing in four social groups (8 adults, 3 subadults, and 4 large immatures). I also make use of the behavioral and demographic data collected by Dr. Linda Fedigan and her students on the white-faced capuchins in Santa Rosa National Park since 1984.

BACKGROUND

Relationships among male nonhuman primates

Perceptions of the "typical" male primate have changed dramatically over the past few decades. Early reports of male relationships stressed aggressive interactions and how this aggression influenced male dominance hierarchies (e.g. Hall & Devore, 1965; Kaufman, 1967; Packer, 1979); males were described as being intolerant of one another and in constant competition for access to mates (e.g. Zuckerman, 1932). Although male relationships in some species are best characterized as being aggressively competitive (e.g. brown capuchins: Janson, 1985; rhesus macaques: Colvin, 1983: savanna baboons: Packer, 1979) there are a small number of species that are characterized by close affiliative relationships among coresident males (chimpanzees: Goodall, 1986; squirrel monkeys: Boinski, 1994; hamadryas baboons: Sigg *et al.*, 1982; red colobus monkeys: Struhsaker, 1985; Stanford, 1998; spider monkeys: Symington, 1990; muriquis: Strier, 1994a). All of these primate species display a social system characterized by male philopatry and female-biased dispersal, which led to an initial assumption that kinship was a necessary precursor for affiliative bonding among males (van Hooff, 2000; van Hooff & van Schaik, 1994).

Although groups characterized by female philopatry and male dispersal are thought to contain unrelated immigrant males, reports of kin-linked immigrations suggest that coresident males may be more closely related than has been previously assumed. There is evidence for kin-linked immigration in vervets and in several species of macaques in which young males have been observed leaving their natal groups together (see Melnick & Pearl 1987, Pusey & Packer 1987; and van Hooff & van Schaik 1994 for reviews). It is also possible that males are migrating towards kin; that is, joining groups containing previously dispersed male kin (van Hooff & van Schaik 1992). However, with the exception of bonnet macaques (Rahaman & Parthasarathy, 1969; Silk, 1994) none of the well studied species characterized by female philopatry and male

dispersal (e.g. cercopithecines), display high levels of affiliation and/or proximity between males (see Perry, 1998 for review). In the case of bonnet macaques, the high levels of affiliative interactions among males have been linked to kinship (Silk, 1992, 1994).

Few studies have focused directly on male relationships within female-philopatric species, and this dearth of available information likely reflects the difficulty of conducting long-term investigations on dispersing individuals. Smith and Sprague (1992) point out that life history observations for males in female-philopatric species, are usually based on anomalous individuals that remain in the social group under observation. This bias is attributable to the inherent difficulty of following individuals that move frequently between groups in free-ranging species. Strier (1994b) also points out that until the early 1990s, studies of male-dispersed species rarely followed up on the fates of dispersing individuals and this has had a significant effect on how we view and interpret data on dispersal (Moore, 1984). For example, the factors influencing a male's decision to emigrate ("push" factors) are much easier to study than the factors influencing his decision of which group to join ("pull" factors) (Smith & Sprague, 1992). Smith and Sprague (1992) argue that push factors can be illuminated through the study of a single group, while pull factors necessitate observations of multiple groups.

Relationships among male capuchins

There are four commonly recognized species within the genus *Cebus*: the white-fronted capuchin (*C. albifrons*), brown or tufted capuchin (*C. apella*), white-faced capuchin (*C. capucinus*), and the wedge-capped capuchin (*C. olivaceus*). These four capuchin species are relatively well known, and a fifth lesser known and recently recognized species, the Ka'apor capuchin (*Cebus kaapori*), has been added to some of the more recent taxonomic lists (see Rowe, 1996). Of the four better known species, all reside in groups comprised of multiple males and females and all are characterized by male-biased dispersal. In general, capuchins are considered female-bonded (Wrangham, 1980) or resident nepotistic (Sterck *et al.*, 1997) in that they exhibit

female philopatry and male dispersal; affiliative bonds among females are generally stronger than they are between females and males, or among males; females develop dominance hierarchies; and, females also appear to be responsible for the direction of group movement (Fragaszy *et al.* in prep). The most conspicuous way that capuchins stray from the original model of female-bonded primates (Wrangham, 1980) resident nepotistic (Sterck *et al.*, 1997), is that at most study sites males, rather than females, are the active participants in encounters with extragroup conspecifics and predators (Fragaszy, *et al.* in prep.).

Although at first glance, the social systems of these four primate species seem remarkably similar, in actuality they are rather diverse, and these difference are mainly attributable to the relationships among coresident males. Male capuchins display an extensive range of variation in their relationships with one another, and this variation exists both among and within species, particularly for the two better studied species: brown capuchins (*C. apella*) and white-faced capuchins (*C. capucinus*). This variation in male relationships likely reflects the behavioral plasticity characteristic of the genus (see Fragaszy *et al.* 1990) and may indicate that male relationships change in response to ecological pressures and/or social pressures occurring within groups (e.g. Janson, 1998). However, with the exception of Perry (1998), whose study concentrated on male relationships within a single group of white-faced capuchins, no studies have focused on male relationships within capuchin groups. Therefore, much of the data currently available on capuchin male relationships are anecdotal and based on *ad libitum* observations.

The first published accounts of male relationships in brown capuchins (*Cebus apella*) reported that alpha males not only monopolized matings within the group, but they also directed high rates of aggression towards subordinate males (Janson, 1985, 1986). Subordinate males remained on the periphery of the group, avoiding interactions with the alpha male and resident females, and did not participate in group defense against either predators or conspecifics (ibid.). These reports led to an initial assumption that brown capuchins reside in what are functionally uni-male social groups. However, additional studies on brown capuchins at multiple study sites

have yielded a much more diverse view of male relationships within this species. For example, Izawa (1980, 1994) reported that male brown capuchins displayed low rates of aggression and he observed frequent affiliation between alpha and subordinate males. The participation of subordinate males in group defense against predators (Izawa, 1980; van Schaik & van Noordwijk, 1989), and the mating success of these males (Janson, 1998), has also been observed.

The relationships among male wedge-capped capuchins (*C. olivaceus*) seem to be less variable than those documented for brown capuchins. Reports of male-male relationships in this species resemble the early reports of brown capuchins; a highly central alpha male who monopolizes matings and keeps subordinate males on the group's periphery (Robinson, 1988). Groups of wedge-capped capuchins do appear to be functionally uni-male, and interactions between subordinate males and group females are described as rarely occurring and agonistic when they do occur (O'Brien, 1991). Given this social structure, it is striking to find that subordinate males of this species do cooperate with the alpha in defending the group during extragroup conflict (Robinson, 1988).

Male relationships within groups of white-fronted capuchins (*C. albifrons*) appear fairly egalitarian in that alpha males do not monopolize access to mates and resources, and relationships among coresident males are generally characterized by low rates of agonism and high rates of cooperation (Defler, 1982; Janson, 1986). This male-male intragroup cooperation has been observed in group defense against predators, during conflicts with other groups of conspecifics, and in resource competition with groups of brown capuchins (Janson, 1986).

Similar to brown capuchins, male relationships in white-faced capuchins (*Cebus capucinus*) have been reported as being highly variable, and this variability not only occurs among study sites, but among groups within the same population (e.g. Santa Rosa). In terms of access to mates and resources, relationships among males are fairly egalitarian, and although a distinct alpha male is discernable within groups, it is the extent to which he asserts his dominance that appears to be most variable (Fragaszy *et al.*, in prep). Perry (1998) reported that the alpha male in her study

group at Lomas Barbudal, Costa Rica, closely monitored the interactions of his subordinate coresident males, and regularly disrupted any affiliative behaviors among them. Several other studies have indicated that male white-faced capuchins spend very little time in close proximity, display low rates of male-male grooming (Santa Rosa: Rose, 1994a; Barro Colorado: Oppenheimer, 1968; Perry, 1995) and Perry (1995, 1998) reports that aggressive behaviors among males far exceed their rates of affiliative behaviors. Fedigan (1993), on the other hand, found that the male white-faced capuchins in her Santa Rosa study groups groomed each other more than they groomed females, and males were, for the most part, affiliative towards one another. Perry (pers. communication), reports that in her new study group in Lomas Barbudal, the rates of affiliative behavior among males are much higher than those observed in her original study group.

In white-faced capuchins, male-male intragroup competition for access to mates has not been documented and the alpha male does not monopolize matings nor does he appear to be the exclusive target of female choice (Fedigan 1993). Another constant that appears in all references to male relationships in white-faced capuchins, is a high rate of male-male cooperation in group defense against both predators and extragroup males (Oppenheimer, 1968; Mitchell, 1989; Fedigan, 1993; Rose, 1994a; Rose & Fedigan, 1995; Perry, 1998; Rose, 1998). This cooperative aggression appears to occur independent of male relationships within groups (Rose, 1998).

Life history of male white-faced capuchins

Studies of New World primates are still in their infancy when compared with the long-term studies conducted on many species of Old World monkeys and apes. To date, no inclusive account of life history patterns in wild capuchins exists in the published literature. Fedigan *et al.* (1996) provide the most informative account on white-faced capuchin life history. Their report is based on a park-wide population of this species (Santa Rosa National Park, Costa Rica) although most of the life-history data included here have been gleaned from years of intensive observation

on three main study groups. The infant sex ratio in the Santa Rosa National Park study groups is 3.6:1.0 in favor of males, with the rate dropping to 2.8M:1.9F for small juveniles (ages 2-4 years), and 1.6M:1.0F in large juveniles (ages 4-6). The mortality rate for infants and immatures under 5 years was 61%, with the highest mortality occurring within the first year (29%). Infant mortality rates were higher for males (22%) than females (0%). The mortality rate for males over five years of age was estimated at 55% (comparing the number of males leaving the study groups vs. entering). When this rate is broken down and examined according to male age class, Fedigan *et al.* (1996) report an adult male mortality rate of 61% while that of subadult (8-10 years) and immature males, was 37.5%.

For males over 5 years, the average tenure within groups is 40.6 months. This finding indicates that males change groups many times throughout their lives, and Fedigan *et al.* (1996) have observed multiple transfers of known males in their study groups. Complete changeovers in male membership have occurred every three to four years since observations began in Santa Rosa (Fragaszy *et al.*, in prep.). However, there are currently no data available on age of emigration or the dispersal patterns of this, or any of the other capuchin species.

Male-bonding in primates

The term male-bonding generally refers to cooperative aggression among coresident males in mutual defense against outsiders (e.g. Stanford 1998; Wrangham & Peterson 1996). In primates, such cooperation among same-sexed coresidents is expected to occur much less easily among males than among females (van Hooff & van Schaik, 1992). The possibility of cooperation among males is reduced due to the very nature of the resource males are competing for - fertilizations which cannot be shared in the same way as food. Male cooperation in group defense is predicted to arise when between group competition for mates is high, making such cooperation necessary to retain group membership and access to females (van Hooff, 2000). The formation of cooperative bonds among males may, in such cases, serve as a strategy for controlling access to

reproduction. High levels of cooperation and tolerance among group living males is a phenomenon observed in several species of social mammals (lions: Packer et al. 1988; cheetahs: Caro 1994), and it appears to be a major factor influencing the formation of long-term male bonds in several primate species (e.g. muriquis: Strier, 1992; chimpanzees: Wrangham & Peterson 1996; red colobus monkeys: Stanford 1995).

According to van Hooff and van Schaik (1994), cooperation and tolerance among group living males can only be predicted to evolve once "the conflict over reproductive interests has become subordinate to other interests" (p.318). That is, coresident males must contend with the problem of access to mates, because overt mating competition among them would interfere with cooperation in other contexts. This problem, according to van Hooff and van Schaik (1992), may be dealt with in some species by males exercising restraint in within group mating competition, resulting in more equitable copulation rates. Common chimpanzees provide one of the strongest examples of male-bonding in nonhuman primates, and although mating competition among males does exist, males are reported to display "remarkable" restraint in their mating competition with co-resident males (van Hooff & van Schaik 1992).

Van Hooff (2000) suggests that "evolutionary logic" leads us to expect that male-bonding would be facilitated by kinship, as males may tolerate and cooperate with other males in order to increase the reproductive success of related co-resident males (see also Mitani *et al.*, 1996). Inclusive fitness benefits may, therefore, be an incentive for such cooperation, and may lead to relaxed intragroup mating competition (van Hooff & van Schaik 1992; Mitani *et al.*, 1996). Male-bonding has, however, been observed in white-faced capuchins; a species in which group males are immigrants and have long been presumed to be unrelated. Cooperative defense by coresident male white-faced capuchins is commonly observed during encounters with predators and neighboring groups (Perry, 1998; Fedigan, 1993), in resisting immigration attempts by extragroup individuals (Perry, 1995; Fedigan, 1993), and in the expulsion of resident males during group takeovers (Fedigan, unpublished data). Male resistance to extragroup males is especially keen and

the cooperation of coresident males during intergroup encounters, and in expelling would-be immigrants, appears to be key in maintaining residence within the group and protecting group females and infants. When male relationships within groups deteriorate, ultimately leading to the emigration of some or all subordinates, it is only a matter of time before a takeover occurs.

But why would these presumably unrelated males, residing together and competing for mates and resources, cooperate with one another? Unrelated males are less likely to cooperate since group living males must struggle with the problem of how to divide matings (van Hooff & van Schaik, 1994). In the absence of male philopatry, kinship among males can be maintained through parallel dispersal (kin-linked migration) (van Hooff, 2000). Parallel dispersal can occur when male siblings emigrate together, or when males preferentially disperse into groups containing familiar, previously dispersed, males. In these cases, the proximate factor influencing the formation of bonds among males would be familiarity and predictability in their relationship (ibid; see also Strier, 1994b). There are reports of young male white-faced capuchins disappearing from their natal groups together (Fedigan, pers. comm.), indicating that kin-linked immigration may be occurring. However, very little is currently known about the dispersal patterns of this species and male life-history patterns have been largely speculative

CONTENTS OF DISSERTATION

In chapters two and three, I examine the patterns and causation of dispersal in male white-faced capuchins. These two chapters summarize the 17 years of behavioral and demographic data collected on several long-term study groups in Santa Rosa National Park, combined with anecdotal accounts of my own observations of dispersing males during my field work in the park. These two chapters present the first comprehensive account of male dispersal patterns for this species, and provide the life history data necessary to evaluate male relationships within groups.

In chapter four, I examine the costs and benefits of male tolerance of multiple coresident males within groups of white-faced capuchins. Specifically, I examine the effect of male

emigration on the social and non-social vigilance of coresident males. In the final data chapter, I analyze male affiliative relationships within my four study groups, comparing male-female and male-male relationships. I then examine male-male dyadic relationships in an attempt to discover what factors are influencing the nature of male relationships in this species. In these latter analyses, I take into account group size, sex ratio, male age, relationship duration, and rank distance. In chapter six, I summarize the key conclusions from my study, relating them to the evolution of cooperative aggression (male-bonding) and the evolution of the multimale social system of white-faced capuchins.

REFERENCES

Boinski, S. 1994. Affiliation patterns among male Costa Rican squirrel monkeys. *Behav.*, 130: 191-209.

Caro, T.M. 1994. *Cheetahs of the Serengeti Plains*. Chicago: University of Chicago Press.

Colvin, J.D. 1983. Influences of the social situation on male emigration. In *Primate Social Relationships: An Integrated Approach* (R.A. Hinde, ed.). Blackwell Scientific Publications, London, pp. 160-171.

Defler, T.R. 1982. A comparison of intergroup behavior in *Cebus albifrons* and *C. apella*. *Primates*, 23:385-392.

Fedigan, L.M. 1993. Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol.*, 14: 853-877.

Fedigan, L.M., Rose, L.M. and Avila, R.M. 1996. See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In: *Adaptive Radiations of Neotropical Primates* (M. Norconk, A. Rosenberger & P. Garber, eds.) Plenum Press, New York, p.289-308.

Fragaszy, D.M., Visalberghi, E & Robinson, J.G. 1990. Variability and adaptability in the genus *Cebus*. *Folia Primatol.*, 54:114-118.

Fragaszy, D., Fedigan, L.M. and Visalberghi, E. (in prep.). Social behavior: Interaction, relationships and social structure. In: *The Complete Capuchin Monkey*. Cambridge University Press, Cambridge.

Goodall, J. 1986. *The Chimpanzees of Gombe*. Cambridge: Harvard University Press.

Hall, K.R.L. and Devore, I. 1965. Baboon social behavior. In *Primate Behavior* (I. Devore, ed.). Holt, Rinehardt, and Winston, New York.

van Hooff, J.A.R.A.M. 2000. Relationships among non-human primate males: a deductive framework. In: *Primate Males: causes and consequences of variation in group composition*, (P.M. Kappeler, ed.) Cambridge University Press, Cambridge, pp.183-191.

van Hooff, J.A.R.A.M. & van Schaik, C.P. 1992. Cooperation in competition: the ecology of primate bonds. In *Coalitions and Alliance in Humans and Other Animals*, (S. Harcourt & F. de Waal, eds.). Oxford University Press, Oxford.

van Hooff, J.A.R.A.M. & van Schaik, C.P. 1994. Male bonds: affiliative relationships among nonhuman primate males. *Behav.*, 130:309-337.

Izawa, K. 1980. Social behavior of the wild black-capped capuchin (*Cebus apella*). *Primates*, 20:57-76.

Izawa, K. 1994. Group division of wild black-capped capuchins. *Field studies of the New World Monkeys, La Macarena, Columbia*, 9:5-14.

Janson, C. H. 1985. Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behav. Ecol. Sociobiol.*, 18:125-138.

Janson, C.H. 1986. The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In *Primate Ecology and Conservation*, (J.G. Else & P.C. Lee, eds.). Cambridge University Press, Cambridge, pp. 169-179.

Janson, C.H. 1998. Capuchin counterpoint. In *The Primate Anthology. Essays on Primate Behavior, Ecology, and Conservation from Natural History*, (R.L. Ciochon & R.A. Nisbett, eds.). Prentice Hall: New Jersey, pp. 153-159.

Kaufmann, J.H. 1967. Social relations of adult males in a free-ranging band of rhesus macaques. In *Social Communications Among Primates* (S.A. Altmann, ed.). Chicago: University of Chicago Press.

Melnick, D.J. & Pearl, M.C.1987. Cercopithecines in multimale groups: genetic diversity and population structure. In: *Primate Societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.) University of Chicago, Chicago, pp. 121-134.

Mitani, J.C., Gros-Louis, J. & Manson, J.H. 1996. Number of males in primate groups: comparative tests of competing hypotheses. *Amer. J. Primatol.*, 38:315-332.

Mitchell, C.L. 1989. *Resources, group behavior, and infant development in white-faced capuchin monkeys,* Cebus capucinus, Ph.D. thesis, University of California, Berkeley.

Moore, J. 1984. Female transfer in primates. *Int. J. Primatol.*, 5:537-589.

O'Brien, T.C. 1991. Female-male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. *Anim. Behav.*, 41:555-567.

Oppenheimer, J.R. 1968. *Behavior and ecology of the white-faced monkey, Cebus capucinus on Barro Colorado Island, Canal Zone.* Ph.D. dissertation, University of Illinois-Urbana, University Microfilms International.

Packer, C. 1979. Intertroop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.*, 27:1-36.

Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J. & Borgerhoff-Mulder, M. 1988. Reproductive success in lions. In: *Reproductive Success*, (T.H. Clutton-Brock, ed.). University of Chicago Press, Chicago, pp.363-383.

Perry, S.E. 1995. *Social relationships in wild white-faced capuchin monkeys (Cebus capucinus).* Ph.D. Thesis, University of Michigan.

Perry, S.E. 1998. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behav.*, 135: 139-172.

Pusey, A. E. & Packer, C. 1987. Dispersal and philopatry. In: *Primate Societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.) University of Chicago, Chicago, pp. 250-266.

Rahaman, H. & Parthasarathy, M.D. 1969. Studies on the social behaviour of bonnet monkeys. *Primates*, 10:149-162.

Robinson, J.G. 1981. Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivitus*. *Anim. Behav.*, 29:1036-1056.

Rose, L.M. 1994a. Benefits and costs of resident males to females in white-faced capuchins (*Cebus capucinus*). *Amer. J. Primatol.*, 32:235-248.

Rose, L.M. 1994b. Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol.*, 15(1):95-114.

Rose, L.M. 1998. *Behavioral ecology of white-faced capuchins (Cebus capucinus) in Costa Rica.* Ph.D. dissertation, Washington University-St. Louis MI, University Microfilms International.

Rose, L.M. & Fedigan, L.M. 1995. Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Anim. Behav.*, 49: 63-70.

Rowe, N. 1996. *The Pictorial Guide to the Living Primates*. Ponganias Press, New York.

van Schaik, C.P. & van Noordwijk, M.A.1989. The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behav. Ecol. Sociobiol.*, 24:265-276.

Sigg, H., Stolba, A., Albegglen, J.J. and Dasser, V. 1982. Life history of hamadryas baboons: Physical development, infant mortality, reproductive parameters, and family relationships. *Primates*, 23:473-487.

Silk, J.B. 1992. Patterns of intervention and agonistic contests among male bonnet macaques. In *Coalitions and Alliance in Humans and Other Animals*, (S. Harcourt & F. de Waal, eds.). Oxford University Press, Oxford, pp. 215-232.

Silk, J.B. 1994. Social relationships of male bonnet macaques: male bonding in a matrilineal society. *Behav.*, 130:271-291.

Smith, E. O. & Sprague, D.S. 1992. Introduction: Migration and Dispersal. *Int.. J. Primatol.*, 13:357-359.

Sprague, J.S. 1992. Life history and male intertroop mobility in Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.*, 13:437-454.

Stanford, C.B. 1998. Predation and male bonds in primate societies. *Behav.*, 135:513-533.

Stanford, C.B. 1995. The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Anim. Behav.*, 49:577-587.

Sterck, E.H.M., Watts, D.P., and van Schaik, C.P. 1997. The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.*, 41:291-309.

Strier, K.B. 1992. *Faces in the Forest: the Endangered Muriqui Monkeys of Brazil*. Oxford University Press, New York.

Strier, K.B. 1994a. Brotherhoods among atelins: Kinship, affiliation and competition. *Behav.*, 130(3-4):151-167.

Strier, K.B. 1994b. Myth of the typical primate. *Yrbk. Phys. Anth.*, 37:233-271.

Struhsaker, T.T. 1985. Infanticide in a patrilineal society of red colobus monkeys. *Zeits. Tierpsych.*, 69:89-132.

Symington, MM 1990. Fission-fusion social organization in *Ateles* and *Pan*. *Int. J. Primatol.*, 11:47-61

Wrangham, R. (1980). An ecological model of female-bonded primate groups. *Behav.*, 75:262-299.

Wrangham, R. & Peterson, D. 1996. *Demonic Males: Apes and the Origins of Human Violence*. Houghton Mifflin Co., New York.

Zuckerman, S. 1932. *The Social Lives of Monkeys and Apes*. New York: Harcourt, Brace.

CHAPTER TWO

Life history of male white-faced capuchins (*Cebus capucinus*) Part 1: patterns and causation of natal emigration.

INTRODUCTION

The majority of mammalian and avian species are characterized by dispersal from the natal group by one or both sexes (Greenwood, 1980). The pattern of male-biased dispersal is most commonly observed among prosimians and the Old World cercopithecines, and more rarely among New World primates (Strier, 1994; see also Strier, 1999 for review). Until recently our knowledge of male life histories were limited to several cercopithecine species (e.g. rhesus macaques: Drickamer & Vessey, 1973; Japanese macaques: Sugiyama, 1976; Sprague, 1992; olive baboons: Packer, 1979; vervets: Cheney & Seyfarth, 1983; etc.). Over the last decade, the results of long term studies on lesser known species have been published, offering a wealth of comparative data on a range of primate taxa (e.g. squirrel monkeys: Mitchell, 1994; ringtailed lemurs: Sussman, 1992; Moor macaques: Okamoto *et al.*, 2000). There remain, however, relatively few reports detailing male life history patterns in free-ranging species characterized by male dispersal, and the monitoring of known individuals through multiple migrations is rare.

Dispersal from the natal group commonly occurs at, or prior to, attaining sexual maturity and is generally assumed to be an evolutionary mechanism for inbreeding avoidance (Itani, 1972: Greenwood, 1980; Melnick & Pearl, 1987; but see Strier, 1994). Determining the proximate cause of natal emigration can, however, be problematic due to the inherent difficulty of following migrating individuals. Several factors have been reported to influence the timing and impetus of natal emigration; those pertinent to male dispersed primate species most frequently involve eviction, and/or an attraction to extragroup individuals (Pusey & Packer, 1987). The eviction of maturing males from their birth group has been most frequently reported in unimale/multifemale langur species. In these cases of eviction, the subsequent dispersal is often the result of aggression from the group's breeding male in response to the increasing maturity of natal males (gray langur:

Mohnot, 1978). Natal eviction has also been observed to occur when a new breeding male takes over a group and continually harasses juveniles until they become peripheral and eventually disperse (e.g. gray langur, Sugiyama 1967; Boggess, 1980; purple faced langurs: Rudran, 1973). However, natal emigration after a group takeover is not always in response to aggression received from the new breeding male. Mathur and Manohar (1990) observed cases where natal male gray langurs "voluntarily" left their group with members of the all-male band upon the new breeding male's arrival.

Attraction to extragroup individuals is a more commonly reported factor influencing male natal emigration, and this attraction may take two forms: sexual attraction to extragroup mates and, in the case of male-dispersed species, an attraction to extragroup males or emigrating group mates (Pusey & Packer, 1987). Attraction to potential mates appears to be the driving force behind male mobility in a number of seasonally-breeding species where the timing of migration coincides with the mating season (vervets: Cheney, 1983; ring tailed lemurs: Sussman, 1992; Japanese macaques: Sprague, 1992). An attraction to extragroup mates may also affect natal male migration in non-seasonally breeding species. Various studies have demonstrated that natal males are not necessarily attracted to groups containing more females, but to groups containing unrelated females (see Pusey & Packer, 1987 for review).

Natal emigration by males has also been reported to occur in response to an attraction to extragroup males or to emigrating group members. In several species of Old World monkeys (patas, geladas, Japanese macaques, and rhesus macaques: see Pusey & Packer, 1987 for review), young males often leave their natal group and temporarily interact with extragroup males (i.e. members of all-male bands, peripheral males of neighboring groups, or solitary males). After a series of such interactions, these males will sometimes emigrate together or join the neighboring group to which they were peripheral (Matsumara, 2000). Maturing natal males have also been observed to emigrate with members of their age cohort or older maternal brothers in several primate species (e.g. Japanese macaques: Sugiyama, 1976; vervets: Cheney & Seyfarth, 1983;

long-tail macaques: van Noordwjick & van Schaik, 1985; see Melnick & Pearl, 1987 for review; ringtailed lemurs: Sussman, 1992). Often referred to as parallel emigration, this coordinated movement of males from the natal group is thought to be a mechanism by which relatedness between male sibs can be maintained in a male dispersed species (van Hooff, 2000).

Capuchins are an anomaly among the New World Primates in that they are characterized by a pattern of male-biased dispersal and female philopatry, and thus more closely resemble the Old World cercopithecines (Strier, 1999). White-faced capuchins fit this general *Cebus* pattern of dispersal and reside year round in groups comprised of multiple adult females, their offspring, and multiple immigrant males (Oppenheimer, 1968; Freese, 1978; Fedigan, 1993). Changes in adult male membership within groups usually occur in the form of takeovers, with complete replacement of group males occurring every 2-4 years (Fedigan, 1993). This frequent replacement of group males indicates that throughout their lives, most male white-faced capuchins will reside in many different social groups. Group takeovers usually involve several extragroup males (2-4) approaching a heterosexual group and eventually supplanting resident males (Fedigan 1993; Rose, 1994; Perry 1995; Rose & Fedigan 1995). During takeovers, the interactions between males are often violent and they have resulted in the eviction of resident males, infanticide, and the deaths or disappearances of both males and females (Fedigan 1993; Rose 1994; Rose and Fedigan 1995). Not all takeover attempts are successful however (Rose, 1998), and male immigrations do occur under less hostile circumstances, with single males approaching the periphery of a group, and eventually joining and being accepted by the group members (Perry, 1996, 1998).

This is the first of two chapters summarizing seventeen years of behavioral and demographic data collected on male white-faced capuchin monkeys (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Together, the two chapters outline the complete life history of male white-faced capuchins. Data presented here provide a detailed description of the timing and circumstances surrounding male natal emigration, while the second chapter details patterns and causation of secondary dispersal, with particular reference to the effects of male age class on these patterns. In

this paper, I examine and describe the conditions under which male natal emigration occurs and attempt to determine the proximate causes of natal emigration in white-faced capuchins and the benefits of the observed dispersal pattern. Specifically, I test the following predication derived from the above review of the literature: (1) if eviction is a primary motivator for male natal emigration, it is expected that male emigration will coincide with group takeovers; (2) if male natal emigration is occurring in response to an attraction to mates, emigrations are expected to occur at sexual maturity and they should be clustered around the "conception peak"(white-faced capuchins are not seasonal breeders but do display a significant birth peak in the dry season, indicating there must also be a conception peak in the wet season); and (3) if natal emigration is in response to the departure of group mates, there should be a high frequency of parallel emigration. It is important to note that these predictions are not necessarily mutually exclusive. For example, a male may disperse with several group mates after the takeover of his natal group, indicating both eviction and attraction to dispersing group mates as proximate factors. However, the relative frequency of the factors and circumstances surrounding natal emigration events, will provide insight into the overall dispersal pattern of this species.

METHODS

Study Site

Data were collected on several groups of wild white-faced capuchins residing in the Santa Rosa Sector of the Area de Conservacion Guanacaste. Formerly known as Santa Rosa National Park (SRNP), the sector was established as a protected area in 1971 and is located near the Nicaraguan border, 35 km northwest of Liberia in Guanacaste Province of Costa Rica. The original boundaries of SRNP encompass approximately 108 km^2 of dry deciduous forest and reclaimed pasture in varying stages of regeneration, and is comprised of several stepped plateaus that range from 300 m in altitude to sea level, where the park is bordered by the Pacific Ocean. The site has been described in detail elsewhere (Fedigan *et al.*, 1996; Fedigan & Jack , in press).

The area experiences two distinct seasons: a dry season from December through May, and a rainy season from June through November. Annual rainfall in the park averages between 800 and 2600 mm (mean = 1472 mm) and mean high temperatures ranging from 21.6°C (September) to 34.4°C (April) (Janzen and Hallwachs 1995).

Species

White-faced capuchins range from as far north as Honduras, throughout Central America, and into northwestern Ecuador (Rowe, 1996). The multimale/multifemale groups of white-faced capuchins are comprised of related females, immigrant males, and their immature offspring. Female-female relationships within groups of white-faced capuchins are maintained over many years and appear to be based on kinship and stable partner preferences for grooming, proximity, and coalitionary support (Perry, 1995; Fragaszy *et al.*, in prep[a].). Males, on the other hand, are transient group members and although this makes the formation of durational bonds between them more difficult, there is some evidence of male-bonding in this species (Chapter 5). Males are approximately 25-35% larger than females and are usually individually dominant to them (Fedigan, 1993). Annual censuses of the capuchin population in SRNP, Costa Rica, have yielded a mean group size of 17.2 with sex ratios approaching equality (Fedigan & Jack, in press). White-faced capuchins are not strict seasonal breeders, but they do display a birth peak between January and April (Fedigan *et al.*, 1996).

Study Groups

Dr. Linda Fedigan, University of Alberta, commenced studies of the white-faced capuchins of SRNP with a short demographic survey in 1982, and more intensive censuses in 1983 and 1984 (Fedigan 1986, Fedigan et al. 1985, Chapman et al. 1988). In 1984, two study groups were selected for intensive research. Individuals residing in these groups were habituated and discrimination between individuals began. In 1985 the SRNP research team commenced

recording births, deaths, and migrations within the study groups (see Fedigan & Rose, 1995) and biweekly observations detailing the groups' foraging and social behavior also began; a practice that continues through the present. These groups have been monitored continuously by Dr. Linda Fedigan and her research team since 1985, with the exception of 21 months spread over five years: a 6 month hiatus in 1991, 3 months in 1995, 4 months in 1996, 5 months in 1997, and 3 months in 1999. Much of the data summarized on the second emigrations of known males (previous natal males from the Los Valles group), come from my own 15 month field study of male white-faced capuchins residing in four social groups within SRNP. Please refer to Appendix A for the location of the home ranges for each study group within central area of the park.

With the exception of the periods specified above, at least 20 hours each month have been spent locating and observing the study groups. Although several members of the original study groups were marked to ease individual identification (Glander *et al.*, 1991), members of Dr. Fedigan's research team have since come to rely on natural markings for this purpose. All individual markings such as scars, poorly healed broken limbs or digits, brow and peak shape, etc. are recorded by observers. When new researchers join the team, these individual identifiers are passed on while in the field, ensuring the identities are correctly assigned. Using this method of identification, individual monkeys have been tracked since 1985 and three generations of females have been observed within one of the long term study groups.

Individuals are also identified according to their age-sex class and the age breakdown used for males in the study groups is as follows: infant 0-24 months; small immature 2-4 years; large immature 4-6 years; subadult 7-10 years; adult $\geq$ 10 years.

Sendero Group (SE):

LMF began observing the SE group in May 1984; however, differentiation between immature individuals was not complete until June, 1986. The group was intensely observed from June 1986 through April 1993, when it dissolved after a series of unsuccessful male takeovers, loss of range

to neighboring groups, and the death and/or emigration of the majority of group members. In 1986 the group contained 12 individuals: 5 adult males, 3 adult females, 2 large immature females, 1 large immature male, and 1 independent male infant. The independent infant is included in the sample of natal SE males, however, the large immature male, present in 1986, has not been included as it is uncertain that he was born into this group. When observations of the SE group began, this male was estimated to be 4 to 6 years of age and it is quite possible that he was an immigrant prior to the start of intensive observations.

NB: The Sendero group's home range fell within the current LV home range (see LV range on map in Appendix A).

Cerco de Piedra Group (CP):

LMF also commenced studies on the CP group in May 1984. Although differentiation between adult individuals was complete in 1986, the sex of infants was not confirmed until 1989. In April 1989, 11 group members disappeared after the group was invaded and taken over by extragroup males (possible group fission). After the takeover, the group consisted of 1 adult male, 1 subadult male, 5 adult females, 2 small immature females, and 2 small immature males. Of the two small immature males, only one was a confirmed CP natal male born in 1987, and the other had immigrated into the group with the invading adult and subadult males, or with a new adult female who appeared in the group shortly after the takeover event. The data presented on the CP group, therefore, includes the male born in 1987 and all new male infants born into the group after April 1989. A large immature male who was also present in the group when observations began in 1985, immigrated to a neighboring group after the 1989 takeover event. His estimated birth year is 1981 and he was omitted from the sample as his natal origin is uncertain.

Los Valles Group (LV):

Intensive observations of the LV group began in 1990 after several members of the CP and SE groups immigrated into LV. The LV group continues to be the focus of intensive study to this day. When observation of the group began, there were 18 groups members present: 3 adult males, 2 subadult males, 4 adult females, 4 large immature males, 1 small immature female, and 4 independent infants (2 males; 2 females). One of the large immature males present in LV in 1990 had previously immigrated from SE, and he is not included in the sample of LV natal males. The 3 remaining large immature males have also been excluded from the sample of LV natal males as they were estimated to be born circa 1985, and it is unclear whether they were natal LV males.

Data Analysis

SPSS-SURVIVAL analysis was used to determine the median age of natal emigration in the study groups. SURVIVAL analysis allows for the use of both completed/uncensored intervals (i.e. males who have emigrated from their natal group) and incomplete/uncensored intervals (males still residing in their natal group as of May 2000, the cut off point for data used). Analysis based solely on complete intervals can result in shorter intervals; that is, it may underestimate the mean age of natal emigration. As used here, SPSS- SURVIVAL generates the median age of male natal emigration while taking into account males who have not yet dispersed from their natal groups. A Binomial test is used to examine seasonal differences in male natal emigration.

RESULTS

Mortality and age of natal emigration

Table 2.1 summarizes the number of males born into each of the three study groups and their subsequent fates (e.g. died, transferred, etc.). In total, 38 males were born during the specified periods, 37% of whom were confirmed (N=8) or suspected dead (N=6). All of these infants disappeared prior to the age of 14 months (mean = 6.3months; range = 1 day to 14 months).

Although it is possible that some of these males survived and entered into new groups, the youngest confirmed age on record for successful natal emigration at this study site is 20 months. This young male transferred into a neighboring group where an older maternal male sibling and a natal age mate had immigrated approximately one month prior to his own transfer.

Three of the males in the sample (8%) were still alive and residing in their natal groups as of May 2000. Their mean age was 37.7 months; the oldest was 53 months, and the youngest was 12 months. Eleven natal males (31%) were confirmed to transfer directly into neighboring groups, while the remaining ten males (28%) disappeared from the study area but were not presumed dead. The mean age of natal emigration/disappearance for these 21 dispersing males was 50 months (4 years, 2 months), ranging from 20 – 96 months. When the three males still residing in their natal groups are included, and censored (incomplete) intervals are assigned to them, SURVIVAL analysis indicates the median age at natal emigration is 54.6 months (N=24).

Season/month of natal disappearance

The month of dispersal was noted for each of the 21 natal males who emigrated from the three main study groups. Those males either suspected or confirmed dead are not included in the data set (N=12), and the males for whom the exact month of departure is unknown (N=5) were divided across the range of possible months. That is, if two males dispersed during a four month period of researcher absence between August and December, 0.5 dispersals were recorded for each of those months. These males have been included in the sample because the majority of periods during which monthly observations were not taken coincided with the rainy season, and I did not want to bias the sample by excluding them. Emigrations occurred throughout the year, although 67% (N=14.33) took place during the dry season months (Dec. through May), while 33% (N=6.67) occurred during the wet season months (June – Nov.) (Figure 2.1). This apparent difference in seasonal migration patterns was not statistically significant (Binomial test, p=.189).

Proximate conditions of natal dispersal

In this section I summarize the immediate circumstances surrounding the emigration of males born into the study groups (N=21 excluding those males confirmed or suspected to be dead). Examination of the data set and the *ad lib* notes recorded by the Santa Rosa research team since 1986, indicate three key circumstances surrounding male natal emigration: (a) a breakdown of relationships between group males (adults and subadults); (b) a series of intergroup interactions; and (c) suspected fissioning of the natal group (several individuals, including adult females, disappeared from the group at the same time). I have also added a fourth, (d) "unknown", category representing disappearances that took place during several periods when the groups were not under bi-weekly observation. Note that none of the natal emigrations in the study population was the direct result of eviction following a takeover of the group by invading males. The most frequently observed circumstance surrounding the disappearance of natal males was (a), a breakdown in the relationships between group males. Such breakdowns involved either the wandering of some of the group's adult males (i.e. visiting neighboring groups), or the actual emigration, death in one case, of older coresident males. In the majority of these cases, all of coresident males, with the exception of the alpha, emigrated from the group. Eight of the natal males in the study groups (38%) dispersed under these conditions; that is, they left with older group males or disappeared during a period when male relationships within the group were unstable. For example, in December 1996 two of the three LV coresident adult males dispersed from the group and four immature and 2 subadult males (5 natal males) accompanied them into neighboring groups, leaving the LV alpha male to defend the group on his own (Rose, 1998).

Another common condition for male natal emigration was to transfer groups following encounters with a neighboring group. The home ranges of capuchins usually overlap between two or more groups (Freese & Oppenheimer, 1981; Rose & Fedigan, 1995; Fragaszy *et al.*, in prep[b]; pers. obs.). Although intergroup encounters do not occur on a daily, or often even a weekly, basis they are a major component of the species' behavioral ecology and social organization (Perry,

1996). Such encounters between neighboring groups are usually hostile, although young males have been observed to stay behind and interact affiliatively with similar-aged individuals of neighboring groups. For example, during the early 1990s the three study groups experienced periods when they would come upon one another every few days. These intergroup encounters were most common during the peak of the dry season when water was scarce (February through May) and the groups would often coincide at the only permanent water hole in the area. In 1991, after a series of such encounters, several of the younger SE males were observed to remain behind and play with the juveniles of the neighboring LV group, despite the somewhat hostile interactions between the adult group members. These young males spent several weeks moving between their natal group and LV, where they eventually settled. Six of the natal males (29%) were observed or strongly suspected (i.e. observed in a frequently encountered neighboring group, but transfer not observed) to transfer between groups following such intergroup interactions.

Although white-faced capuchins are characterized by male-biased dispersal, females also disappear from the study groups on occasion. Several females have been observed to leave their group with an ousted alpha male and immature offspring after a changeover of males in their groups (Rose, 1998; pers. obs.), and it is suspected that new groups form through the fissioning of larger, unstable groups (Oppenheimer, 1968). Four of the natal males in the sample (19%) are suspected to have dispersed as a result of a fissioning of their group. For example, two of the younger LV natal males, Frost and Snow, disappeared together from the group with an immigrant subadult male, and an adult female (Snow's mother). An adult male and adult female (Frost's mother) also disappeared from LV two months earlier. With the exception of the adult male who was observed five years later as a member of a distant group, the exact fate of the dispersing LV members is uncertain. However, the circumstances surrounding their disappearances *en masse* do suggest that fission occurred in the group.

The three remaining natal males in the sample (14%) disappeared during periods when monthly observations were not being conducted and the factors surrounding their departures are unknown. Of these three males, the two youngest (Chilero, 24 months and Salt, 35 months) disappeared with a low-ranking adult male during a three week period when researchers were absent from the park in December 1998. Another natal male, Squeaky, disappeared from CP with an adult female (Patch) who was likely his mother (they affiliated regularly and she was part of his natal group when the study began in 1985). The latter two animals were missing following the 6 month period in 1991 during which no observations were made on the groups. It is interesting to note, however, that two months prior to the last observation of Squeaky and Patch, Patch's four day old infant was killed by the alpha male who had taken over the group three months earlier. The infant was killed during a fight between Patch and the alpha male, and Squeaky was a key participant, defending Patch throughout the fight. It is possible that this fight and infanticide influenced the disappearance of these two animals.

In summary, 38% (N=8) of the natal males emigrated when relationships between coresident males began to break down; 29% (N=6) transferred into neighboring groups following a series of intergroup encounters; 19% (N=4) were suspected to have left their natal groups as part of a group fission; and the remaining 14% (N=3) disappeared for unknown reasons during a period of observer absence (Table 2.2).

Frequency of parallel emigration

Of the 21 natal male emigrants, 16 emigrated in the company of at least one other group mate and an additional male joined a group containing familiar individuals. Table 2.3 summarizes the frequency of the observed dispersal patterns: 13 males emigrated with one or more adult/subadult coresident males; two brothers (aged 6.7 and 2 years) disappeared together with their mother and another adult female; one male joined a previously transferred older brother and male age-mate in

a neighboring group; and, one male disappeared with an adult female who was quite possibly his mother. The remaining four natal emigrants (19%) dispersed from their birth groups on their own

Parallel emigration can occur in two main ways: first, when maternal siblings or members of the same age cohort (possible paternal siblings) migrate together or, second, when migrating males enter groups containing familiar, previously dispersed, males from their natal group (Altmann, 1979; van Hooff, 2000). Fifteen (71%) of the natal emigrations were thought, or known, to be parallel. Note that this total excludes one natal male who disappeared with two recent immigrants into his natal group, as it is unlikely that the three males were related. Eleven of the dispersing natal males were observed following their transfer into their next group. Of these confirmed transfers, nine (82%) were parallel.

Subsequent emigration of known natal males

Several of the natal males in the data-set transferred between study groups, enabling us to track their subsequent emigration activity. In total, 10 natal males from two of the main study groups (SE and LV) were observed through their second emigration. The second emigration of these males occurred at a mean age of 96 months (8 years) and their mean tenure in their second group was 38 months. Seven of these males (70%) engaged in parallel dispersal for their second migration. For example, Hank and Finnigan, both LV natal males, dispersed from their second group alone, but subsequently entered into a neighboring group containing a former LV alpha male. In Finnigan's case, he followed Hank into this third group a month after Hank's initial disappearance, also joining the familiar alpha male who was quite possibly his father (i.e. this male was the LV alpha when Finnigan was conceived).

DISCUSSION

The emigration of male white-faced capuchins from their birth groups appears to be in response to three main circumstances: frequent interactions between neighboring groups, the

breakdown of relationships between resident males, and a fission of the natal group. To determine the proximate cause of natal emigration in this species, I investigate these circumstances in light of the predictions set forth in the introduction. My review of the long-term behavioral and demographic data collected on the capuchins in Santa Rosa National park indicates that eviction, in the context of a group takeover, was not a direct cause of natal emigration in the study population. None of the 21 natal emigrations summarized here occurred following the takeover of the natal group by extragroup males. Although eviction of natal males during non-takeover times was not examined due to the nature of the data set, it seems equally unlikely as aggression within groups is very low (pers. obs.). I have observed many occasions where coresident males and females, particularly alpha males, actively search for the missing natal males by emitting special long-distance lost calls (see Perry, 1998). Shortly after their initial dispersal, natal males are also tolerated as occasional "visitors" within their natal group. During these visits the young males are groomed and inspected by the majority of group members and these interactions are highly affiliative, rather than aggressive (pers. obs.).

I predicted that if males are emigrating from their natal group due to an attraction to extragroup mates, emigration should occur at or near the age of sexual maturity. Male natal emigration in the Santa Rosa study groups was confirmed to occur as early as 20 months and as late as 96 months, with a median of 54.6 months (~4.5 years). Male white-faced capuchins do not attain sexual maturity until approximately 8 years of age (Freese & Oppenhiemer, 1981), which, with the exception of the upper age limit of natal emigration observed in the Santa Rosa study groups, is well above the sample mean of 4.5 years. However, data on captive representatives of this species are needed for confirmation of this estimate, as great variation in age at sexual maturity has been reported for captive males of the closely-related tufted capuchin (*Cebus apella*). For example, Fragaszy and Adams-Curtis (1998) found that males in their captive study population were reproducing for the first time by 4 years 5 months while Patino *et al.* (1996) and Nagle and Denari (1982) report that males in their colonies are not capable of reproduction prior

to 7 years. No comparable captive data are currently available for male white-faced capuchins; however, it should be noted that, in general, the Santa Rosa population displays a slower life history than captive tufted capuchins (compare Fedigan *et al.*, 1996 with Fragaszy & Adams-Curtis, 1998). The youngest male confirmed to mate within the study groups (i.e. ejaculation was confirmed) was a 6 or 7 year old immigrant male (Rose, pers. comm.). It is possible that 4.5 years represents the lower limit of reproductive ability for male white-faced capuchins and this age of natal emigration may have evolved in response to breeding potential and, therefore, inbreeding avoidance.

Regardless of the timing of sexual maturity in white-faced capuchins, males emigrate many years prior to attaining full body size, a common occurrence in many male-dispersed primate species (van Noordwijk & van Schaik, 1985; Pusey & Packer, 1987). It is interesting to note that the upper limit observed for age at natal emigration in the SRNP population, 96 months (8 years), was also the mean age of males observed through their second emigrations. At 8 years, male white-faced capuchins are classified as subadults and it is at this age that they begin to undergo noticeable changes in their social interactions and physical appearance. During the subadult phase, young males begin to spend more time interacting with adult females in their groups (non-kin, as all males have emigrated from their natal groups by this age), less time playing, and generally display behavior more on par with that of adult males (KMJ unpub. data). Between the ages of 8 and 10 years, male capuchins also begin to fill out, changing from the long and lanky physique of a juvenile, and approximating the more robust frame of an adult male. Observations of known natal males in SRNP confirm that they do not attain full adult male body size until about 10 years of age.

I also predicted that if natal dispersal was in response to an attraction to extragroup mates, the timing should coincide with the mating/conception season. Such coordination in the timing of dispersal has been observed for a number of seasonally breeding primate species (Pusey & Packer, 1987; Sprague, 1992; Sussman, 1992). Although white-faced capuchins are not

considered seasonal breeders, they do display a significant birth peak between January and April (Fedigan *et al.* 1996) and, therefore, there must also be a peak in the timing of conception. Gestation in this species is estimated at approximately six months (ibid.), indicating that many females are conceiving during the rainy season (July – November). The majority of natal emigrations in SRNP study groups occurred during the dry season. This observation, together with the finding that natal males are likely dispersing prior to sexual maturity, and many years prior to attaining physical maturity, suggests that mating opportunities, and an attraction to extragroup mates, may not be an initial trigger for natal emigration.

The data point instead to an attraction to extragroup males or dispersing group mates. Twenty-nine percent of the natal males dispersed following intergroup encounters and observations of natal males emigrating together and/or into groups containing individuals familiar to them, has been frequently observed. In fact, the data collected on the SRNP capuchins demonstrate that male natal emigration is rarely a solitary event. Among the 21 migrating males in the natal sample, 17 dispersed in the company of at least one other group mate. These 17 males represent 81% of the surviving natal male sample, and all but two of the 11 confirmed natal transfers were parallel. That is, 82% of confirmed male migrations were in the company of maternal siblings, members of their age cohort, and/or into groups containing familiar males. The frequency of parallel emigration among the natal males observed through their second emigration (70%), further illustrate the importance of this dispersal pattern for male white-faced capuchins.

Although the benefits of dispersal, in terms of inbreeding avoidance, may be high, migration also comes with risks. Dispersing individuals will likely be at higher risk of predation, aggression from unfamiliar conspecifics, or even starvation once they leave their familiar natal area in search of a new social group (e.g. Gartlan 1975; Dittus 1977; van Schaik, 1983). The high frequency of parallel emigration observed among male white-faced capuchins indicates that the benefits of this dispersal pattern must be high. Familiarity and predictability in relationships may be an important benefit of parallel dispersal (van Hooff, 2000), and dispersing in the company of other individuals

provides added protection from vulnerability to predation and attacks by extragroup individuals (Sussman, 1992). This dispersal pattern seems to be particularly important for male white-faced capuchins as they approach physical maturity because the cooperation of adult males appears to be crucial in entering new groups where resident males are present (see Chapter 3). The long term data from SRNP also indicate that males have difficulty in retaining group membership without the support that coresident males provide (Rose & Fedigan, 1995; see also Chapter 3). Once an alpha male loses the support of his coresident males, and these males disperse leaving the alpha to defend the group on his own, it is only a matter of time before invading males take over.

However, one of the most important benefits of parallel dispersal may be increased inclusive fitness. Given the observations of male cooperation within groups, particularly in the context of group defense during intergroup aggression (Perry, 1996), and the open mating system of this species (Manson *et al*., 1997), it may be in a male's best interest to reside in groups with related males. Relatedness between males residing in the LV and CP study groups from 1993 – 2000 are currently being analyzed through the amplification of microsatellite markers obtained from follicular and fecal DNA. Given the high frequency of parallel emigration reported here, it is reasonable to assume a high degree of relatedness between group males even in the absence of these genetic data. Moore (1992) suggests that natal individuals dispersing together and subsequently joining the same group, as has been observed among white-faced capuchins, may result in a level of relatedness within the new group that is comparable to that found in groups made up philopatric individuals. In her discussion of age cohorts, Altmann (1979) stresses the importance of considering the relatedness not only between maternal siblings, usually half siblings when male tenure in groups is short, but also between members of an age cohort. Members of an age cohort are likely to be closely related, either as half sibs if there is only one breeding male, or to a slightly lesser degree when several males are siring a cohort (ibid.), as appears to be the case for white-faced capuchins.

A high degree of relatedness between females within the Santa Rosa study groups is also apparent, and may indicate even higher levels of relatedness between natal individuals. For example, in May 2000, the CP study group contained 10 individuals: 2 adult males, 4 adult females, 3 immature females, and 1 immature male. With the exception of the two immigrant adult males, and one of the adult females, all 7 remaining group members are direct descendants of the alpha female (daughters, grand daughters, and son). In the absences of positive genetic evidence, the degree of relatedness between male age cohorts is uncertain. Given the small size of capuchin groups in SRNP (mean = 17.2: Fedigan & Jack, in press), the male-biased dispersal pattern, and the relatedness of individuals within the best-known study group (CP), it is likely that the degree of relatedness among group females and, subsequently, among their offspring, is quite high. The frequency of parallel emigration, even during secondary emigration (Chapter 3), indicates possible relatedness between dispersing and resident males.

The analyses of male life history patterns indicate that male white-faced capuchins, like many male-dispersed species, are very transient group members (Fedigan *et al.*, 1996; Chapters 2 and 3). Their lives are characterized by frequent movement between groups. In the sample of natal males followed through their second dispersal, the mean tenure in their second group was 38 months (3 years, 2 months), demonstrating that upon leaving the natal group, immature males have already entered into the adult male life history pattern of frequent group transfer. As the long-term investigation of white-faced capuchins continues in SRNP, our ability to interpret the complicated life history of this long-lived species can only become clearer.

Table 2.1 Number of males born into study groups and their fates.

	Dead	Transferred	Disappeared	Not dispersed	Total
Sendero (1986-1992)	4	5	0	0	9
Cerco de Piedra (1989-2000)	5	0	5	1	11
Los Valles (1990-2000)	5	6	5	2	18
Total	14	11	10	3	38

Table 2.2. Frequency of proximate conditions of natal emigration.

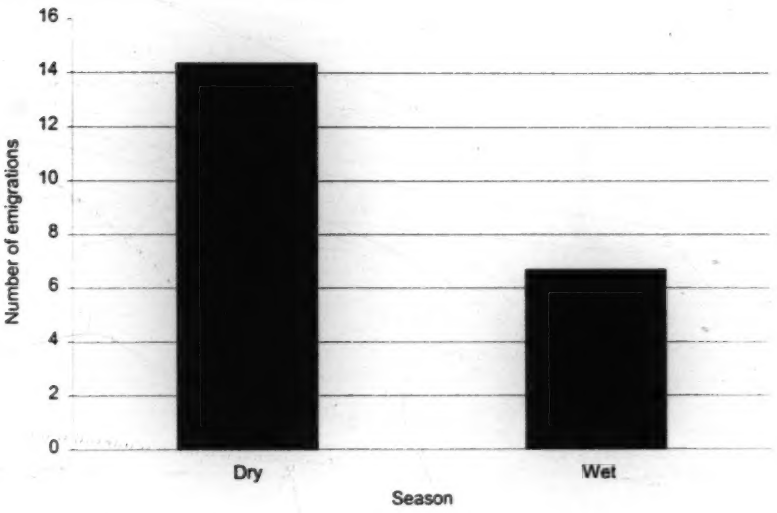
	Sendero	Cerco de Piedra	Los Valles	Total
Breakdown of male relationships	1	2	5	8
Intergroup interactions	4	0	2	6
Takeover	0	0	0	1
Group fission suspected	0	2	2	4
Unknown	0	1	2	3
Total	5	6	11	21

Table 2.3 Frequency of observed dispersal patterns

	Number of observations
With coresident males	15
Joins familiar male(s)[a]	1
With non-male coresidents	1
Alone	4
Total	21

a. dispersing male enters into a group containing a familiar male

Figure 2.1 Seasonal pattern of male natal emigration.



REFERENCES

Altmann, J. 1979. Age cohorts as paternal sibships. *Behav. Ecol. Sociobiol.*, 6:161-164.

Boggess, J. 1980. Intermale relations and troop male membership changes in langurs *Presbytis entellus*in Nepal, *Int. J. Primatol.*, 1:233-274.

Chapman, C., Fedigan, L.M. and Fedigan, L. 1988. A comparison of transect methods of estimating population density of Costa Rican primates. *Brenesia*, 30: 67-80.

Cheney, D.L. 1983. Proximate and ultimate factors related to the mechanism of male migration. In *Primate Social Relationships: An Integrated Approach*, Hinde, R.A. ed. Oxford: Blackwell.

Cheney, D.L. and Seyfarth, R.M. 1983. Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *Amer. Naturalist*, 122:392-412.

Dittus, W. 1977. The social regulation of population density and age-sex distribution in the toque monkey. *Behav.*, 63:281-322.

Drickamer, L.C. and Vessey, S.H. 1973. Group changing in free-ranging male rhesus monkeys. *Primates*, 14: 359-368.

Fedigan, L.M. 1986. Demographic trends in the *Alouatta palliata* and *Cebus capucinus* populations of Santa Rosa National Park. In: *Primate Ecology and Conservation*, Vol. 2 Else, J.G. and Lee, P.C. eds. pp.287-93. Cambridge: Cambridge Univ. Press.

Fedigan, L.M. 1993. Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol.*, 14: 853-877.

Fedigan, L.M., Fedigan, L. and Chapman, C.A. 1985. A census of *Alouatta palliata* and *Cebus capucinus* in Santa Rosa National Park, Costa Rica. *Brenesia*, 23: 309-22.

Fedigan, L.M. and Rose, L.M. 1995. Interbirth interval variation in three sympatric species of Neotropical monkey. *Amer. J. Primatol.*, 37:9-24.

Fedigan, L.M., Rose, L.M. and Avila, R.M. 1996. See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In: *Adaptive Radiations of Neotropical Primates* (M. Norconk, A. Rosenberger & P. Garber, eds.) Plenum Press, New York, p.289-308.

Fedigan, L.M. and Jack, K.M. in press 2001. Neotropical primates in a regenerating Costa Rican dry forest: A comparison of howler and capuchin population patterns. *Int. J. Primatol*, 22(5): 689-713.

Fragaszy, D.M. and Adams-Curits, L.E. 1998. Growth and reproduction in captive tufted capuchins (*Cebus apella*). *Amer. J. Primatol.*, 44:197-203.

Fragaszy, D., Fedigan, L.M. and Visalberghi, E. (in prep.) [a]. Social behavior: Interaction, relationships and social structure. In: *The Complete Capuchin Monkey*. Cambridge University Press, Cambridge.

Fragaszy, D., Fedigan, L.M. and Visalberghi, E. (in prep.)[b]. How do capuchins make a living? Behavioral ecology. In: *The Complete Capuchin Monkey*. Cambridge University Press, Cambridge.

Freese, C.H. 1978. The behavior of white-faced capuchins (*Cebus capucinus*) at a dry-season waterhole. *Primates*, 19: 275-286.

Freese, C.H. and Oppenheimer, J.R. 1981. The capuchin monkey, genus *Cebus*. In: *Ecology and Behaviour of Neotropical Primates*, vol. 1 (Coimbra-Filho, A.F. and Mittermeier, R.H., eds.) pp. 331-390. Academia Brasilia, Rio de Janeiro.

Gartlan, J.S. 1975. Adaptive aspects of social structure in *Erythrocebus patas*. In: *Proceedings from the Symposia of the Fifth Congress of the International Primatological Society*, ed. S. Kondo, M, Kawai, A. Ehara, and S. Kawamura, Japan Science Press, Tokyo.

Glander, K.E., Fedigan, L.M., Fedigan, L.M. and Chapman, C.A. 1991. Capture techniques for three species of monkeys in Costa Rica. *Folia primatol.*, 57: 70-82.

Greenwood, P.J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.*, 28: 1140-1162.

van Hooff, J.A.R.A.M. 2000. Relationships among non-human primate males: a deductive framework. In: *Primate Males: causes and consequences of variation in group composition*, (P.M. Kappeler, ed.) Cambridge University Press, Cambridge, p.183-191.

Itani, J. 1972. A preliminary essay on the relationships between social organization and incest avoidance in non-human primates. In: *Primate Socialization*. New York: Random House, pp. 165-171.

Janzen, D.H. and Hallwachs, W. 1995. Indicative weather data for the Santa Rosa area and Volcan Cacao. Unpublished ms.

Manson, J.H., Perry, S. & Parish, A.R. 1997. Nonconceptive behavior in bonobos and capuchins. *Int J. Primatol.*, 18:767-786.

Mathur, R. & Manohar, B.R. 1990. Departure of juvenile males in *Presbytis entellus* from the natal group. *Int. J. Primatol.*, 12(1):39-43.

Matsumura, S. 2000. Intergroup affiliative interactions and intergroup transfer of young male Japanese macaques (*Macaca fuscata*). *Primates*, 34:1-10.

Melnick, D.J. and Pearl, M.C.1987. Cercopithecines in multimale groups: genetic diversity and population structure. In: *Primate Societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.) University of Chicago, Chicago, pp. 121-134.

Mitchell, C.L. 1994. Migration alliances and coalitions among adult male South American squirrel monkeys (*Saimiri sciureus*). *Behav.*, 130:169-190.

Mohnot, S.M. 1978. Peripheralization of weaned male juveniles in *Presbytis entellus*. In: *Recent Advances in Primatology*, vol. 1, Chivers, D.J. and Herbert, J., eds. Academic Press, New York.

Moore, J. 1992. Dispersal, nepotism, and primate social behavior. *Int. J. Primatol.*, 13:361-378.

Nagle, C.A. and Denari, J.H. 1982. The reproductive biology of capuchin monkeys. *Inter. Zoo Yrbk.*, 22:143-150.

van Noordwijk, M.A. and van Schaik, C.P. 1985. Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). *Anim. Behav.*, 33:849-861.

Okamoto, K., Matsumura, S. and Wantanabe, K. 2000. Life history and demography of wild moor macaques (*Macaca maurus*): Summary of ten years observations. *Amer. J. Primatol.*, 52:1-12.

Oppenheimer, J.R. 1968. *Behavior and ecology of the white-faced monkey, Cebus capucinus on Barro Colorado Island, Canal Zone*. Ph.D. dissertation, University of Illinois-Urbana, University Microfilms International.

Patino, E., Borda, J.T., and Ruiz, J.C. 1996. Sexual maturity and seasonal reproduction in captive *Cebus apella*. *Lab. Primate Newsletter*, 35:8-10.

Packer, C. 1979. Intertroop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.*, 27:1-36.

Perry, S.E. 1995. *Social relationships in wild white-faced capuchin monkeys (Cebus capucinus)*. Ph.D. Thesis, University of Michigan.

Perry, S.E. 1996. Intergroup encounters in wild white-faced capuchin monkeys, *Cebus capucinus*. *Int. J. Primatol.*, 17: 309-330.

Perry, S.E. 1998. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behav.*, 135: 139-172.

Pusey, A. E. and Packer, C. 1987. Dispersal and philopatry. In: *Primate Societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.) University of Chicago, Chicago, pp. 250-266.

Rose, L.M. 1994. Benefits and costs of resident males to females in white-faced capuchins (*Cebus capucinus*). *Amer. J. Primatol.* 32: 235-248.

Rose, L.M. and Fedigan, L.M. 1995. Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Anim. Behav.*, 49: 63-70.

Rose, L.M. 1998. *Behavioral ecology of white-faced capuchins (Cebus capucinus) in Costa Rica.* Ph.D. dissertation, Washington University-St. Louis MI, University Microfilms International.

Rowe, N. 1996. *The Pictorial Guide to the Living Primates*. Ponganias Press, New York.

Rudran , R. 1973. Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. *Folia Primatol.*, 19:166-192.

van Schaik, C.P. 1983. Why are diurnal primates living in groups? *Behaviour* 87: 120-144.

Smith, E. O. and Sprague, D.S. 1992. Introduction: Migration and Dispersal. *Int.. J. Primatol.* 13:357-359.

Sprague, J.S. 1992. Life history and male intertroop mobility in Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.*, 13:437-454.

Strier, K.B. 1999. Why is female kin bonding so rare? Comparative sociality of Neotropical primates. In: *Comparative Primate Socioecology*, P.C. Lee (ed.), Cambridge University Press, Cambridge.

Strier, K.B. 1994. Myth of the typical primate. *Yrbk. Phys. Anth.*, 37:233-271.

Sugiyama, Y. 1967. Social organization of hanuman langurs. In: *Social communication among primates*, Altmann, S.A. ed. University of Chicago Press, Chicago.

Sugiyama, Y. 1976. Life history of male Japanese monkeys. In: *Advances in the Study of Behavior, Vol. 7* (Rosenblatt, J.S. ed.) Academic Press, New York, pp.255-284.

Sussman, R.W. 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *Int. J. Primatol.*, 13:395-413.

CHAPTER THREE

Life history of male white-faced capuchins, Part II:
Effects of age class on patterns and causation of dispersal.

INTRODUCTION

Capuchins (*Cebus*) are unusual among New World primates in displaying a pattern of male biased dispersal, whereas the vast majority of the New World primate genera are characterized by either male philopatry and female dispersal, or bisexual dispersal (Strier, 1999). Therefore, in terms of migration patterns, capuchins more closely resemble the Old World cercopithecines, with females remaining in their birth troop and males dispersing prior to reaching sexual maturity. Long term studies of white-faced capuchins (*Cebus capucinus*) have demonstrated that within groups, male tenure is short and males appear to change groups continuously throughout their lives (Fedigan *et al*, 1996). This pattern of multiple migrations by male primates has also been observed among several cercopithecine species, and male migration patterns and strategies have been reported to differ according to the maturity of individuals (e.g. Sugiyama, 1976; Cheney & Seyfarth, 1983; Sprague, 1992; Strier, 2000a). For example, in most primate species natal emigration occurs prior to sexual and/or physical maturity (Chapter 2; Itani, 1972; see Melnick & Pearl, 1987 for review). Dispersing young natal males are usually unable to attain high ranks within new groups, as they have not yet achieved the physical strength necessary to defeat the dominant adult males (Cheney & Seyfarth, 1983; van Noordwijk & van Schaik, 1985; Sprague *et al*., 1998). Secondary dispersal, on the other hand, typically occurs once a male has attained physical maturity and immigrating males are then able to compete with resident males and enter into a group at a higher rank (van Noordwijk & van Schaik, 1983; Strier, 2000a).

Regardless of their age, entering a new group is a stressful occasion (Alberts *et al*., 1992; Alberts & Altmann, 1995) and males can exact their entry in several ways. In species characterized by a single breeding male, male entrance into a social group requires the defeat of the resident male, and this most often occurs through aggressive interactions (Hrdy, 1977; see

Pusey & Packer, 1986 for review). In multimale species, several options exist for entering into new groups. Males can enter by force, assuming dominant positions within the group, a pattern observed among baboons (Packer, 1979) and long-tailed macaques (van Noordwijk & van Schaik, 1985). The eviction of resident males following group takeovers by multiple males has also been noted in white-faced capuchins (Fedigan, 1993) but has not been commonly reported in other multimale species. More frequently, males from species with multimale social systems enter into groups unobtrusively, and in these cases they initially assume lower ranks in the existing dominance hierarchy (e.g. Japanese macaques: Sugiyama & Ohasawa, 1975; Sprague, 1992; vervets: Henzi & Lucas, 1980; long-tailed macaques: van Noordwijk & van Schaik, 1985). Some species exhibit both patterns of male immigration (aggressive and unobtrusive), even in adulthood (long-tailed macaques: van Noordwijk & van Schaik, 1985; white-faced capuchins: Perry, 1996; Fedigan, 1993), although there is still little known about the factors influencing the way in which males enter into groups and if these vary according to male age.

The proximate cause of male emigration may also change with differing stages in a male's life history. Dispersal is presumed to reflect a male's attempt to increase his reproductive success (Alberts & Altmann, 1995); however, this may be a more important consideration for older males. For example, males emigrating for the first time may be more concerned with dispersing group mates, or joining groups containing familiar males, than are older migrants (Pusey & Packer, 1986 and refs. sited therein). Long term data from several cercopithecine species have demonstrated that immature emigrants not only tend to settle into groups closer to their natal home range, but they also display a greater tendency to disperse with familiar group mates, than do older males (Cheney & Seyfarth, 1983; van Noordwijk & van Schaik, 1985). By dispersing together, males may decrease not only their vulnerability to predators (they have a better chance of spotting a predator) but they may also reduce their risk of attack by adult males (Sussman, 1992) to which young males are more vulnerable than adults (Cheney & Seyfarth, 1983). In contrast, it appears that the factors or conditions influencing male secondary emigration are more

likely associated with maximizing reproductive opportunities. Sussman (1992) found that adult male ringtailed lemurs preferentially transferred into groups with more favorable sex ratios, and studies of several species of Old World monkeys have demonstrated that males often disperse in an attempt to increase their rank which may confer increased access to mates (Altmann & Altmann, 1970; Henzi & Lucas, 1980; Cheney & Seyfarth, 1983).

This is the second paper in my investigation of the migration patterns of male white-faced capuchins in Santa Rosa National Park, Costa Rica. The first of these papers focused on the emigration of natal males and the proximate factors influencing their dispersal. In this paper I focus mainly on secondary dispersal, addressing the effect that the varying stages of male life history may have on migration patterns. First I examine the ways that males enter into groups. Are they using cooperative aggression, forcing their way into groups and evicting resident males, or are they moving in peacefully and joining the resident males already present in the group? Does the way in which a male enters into a group change with age? Second, I examine male tenure within groups to determine if age class influences how long a male remains in any one group. Finally, I investigate the proximate reasons for secondary emigration and determine if these differ according to male age class. To address this last question, I examine the circumstances surrounding male emigration. Specifically, I attempt to determine if male emigration is in response to the following factors: eviction from the group (i.e. males disperse after a takeover); an attraction to extragroup mates (i.e. moving into groups with more favorable sex ratios; increasing rank through group transfer; dispersing during the mating peak); or an attraction to extragroup males or dispersing group mates (i.e. dispersing with group mates or into groups containing familiar males). These data are then combined with those compiled on the patterns of male natal dispersal, to provide a more complete picture of the life history of male white-faced capuchins.

METHODS

Study Site

Data were collected in the Santa Rosa Sector of the Area de Conservacion Guanacaste, located in Northwestern Costa Rica. Protection of this sector, formerly known as Santa Rosa National Park (SRNP), began in 1971, the original boundaries of which encompass approximately 108 km^2 of dry deciduous forest and reclaimed pasture in varying stages of regeneration. SRNP ranges from 300 m in altitude to sea level, where the park is bordered by the Pacific Ocean (for a detailed description of the site see Fedigan *et al.*, 1996; Fedigan & Jack, in press). The area experiences two distinct seasons: a dry season from December through May, and a rainy season from June through November. Annual rainfall in the park averages between 800 and 2600 mm (mean = 1472 mm) and mean high temperatures ranging from 21.6 degrees C (September) to 34.4 degrees C (April) (Janzen and Hallwachs 1995).

Species

White-faced capuchins reside in groups comprised of multiple immigrant males, related females and their immature offspring. Group sizes average approximately 17 individuals with sex ratios approaching parity (Fedigan & Jack, in press). Due to the philopatric nature of females and the formation of long term affiliative relationships observed between them, the species is described as female-bonded (Fragaszy *et al.*, in press). However, the maintenance of long-term affiliative or neutral bonds between males has also been described for this species (Chapter 5). Adult male white-faced capuchins are larger than adult females (25-35%) and individually dominant to them (Fedigan, 1993). White-faced capuchins frequently engage in nonconceptive mating (Manson *et al.*, 1996) and although they are not strict seasonal breeders, they do display a birth peak between January and April (Fedigan *et al.*, 1996). Given that gestation is estimated at six months (ibid.) there must also be a peak in the timing of conception falling between July and November. Although there has been little published about the mating behavior of white-faced

capuchins, it does appear that female choice plays a role, as females solicit and mate with low ranking males (Fedigan, 1993). The mating behavior of subordinate males appears to be largely tolerated by dominant males and clear cases of mate guarding by the alpha male have only rarely been observed (KMJ pers. obs.). These observations indicate that mating within groups of white-faced capuchins is egalitarian in nature; however, only paternity analysis, which is currently underway, will confirm whether or not reproductive success is monopolized by dominant males as has been reported for wedge-capped capuchins (see Strier 2000b, for review)

Study Groups

Dr. Linda Fedigan, University of Alberta, began observing the white-faced capuchins in SRNP in 1982 with a short demographic survey, with more intensive park-wide censuses were conducted in 1983 and 1984 (Fedigan 1986, Fedigan et al. 1985, Chapman et al. 1988). Behavioral observations of two main study groups began in 1984 with the habituation of, and discrimination between, individuals. Records of births, deaths, and migrations began in 1985 with the commencement of biweekly behavioral observations (see Fedigan & Rose, 1995). These observations have continued through the present, with additional groups being added over the years. The study groups have been monitored continuously by a team of researchers since 1985 and, with the exception of several short intervals, at least 20 hours each month have been spent locating and observing them. The ranks of adult and subadult males within study groups have been reported by the Santa Rosa research team since 1984 based on the direction of submissive signals and supplant-avoid interactions between male dyads. Observations of male dominance interactions have been made during focal and *ad libitum* data collection.

Group members are individually identified according to natural markings such as brow shapes, scars, freckles, etc. These individual identifiers have been passed on from researcher to researcher in the field to ensure that identities are correctly assigned. Individuals are also identified according to their age-sex class. The age break-down for male white-faced capuchins

used in this paper is as follows: infant 0-24 months; small immature 2-4 years; large immature 4-7 years; subadult 7-10 years; adult ≥ 10 years.

The majority of descriptive data referred to throughout this paper, came from my own observations during the period of January 1998 through June 1999. During this period, I collected behavioral data on all males ≥ 4 years of age residing in four study groups, and spent a minimum of 60 hours per month with each of the groups. A fifth group was added for a two month period in 1999 (Feb. – Mar.), following the transfer of two males from one of my study groups. Please refer to the Appendix A for the relative locations of each of the study groups detailed below.

Sendero Group (SE):

Although observations of the Sendero group began in 1984, differentiation between immature individuals was not complete until June 1986. This group was observed from June 1986 through April 1993, when it became extinct after the death and/or emigration of the majority of group members following several unsuccessful male takeovers and a loss of range to neighboring groups. Data reviewed here utilize this long term data for the period from June 1986 through April 1993. In 1986 the group contained 12 individuals: 5 adult males, 3 adult females, 2 large immature females, 1 large immature male, and 1 independent male infant. All of these original adult males, and the large immature male, have been included in our sample of immigrant males. The data summarized here incorporate these 7 years of behavioral and demographic data, during which time 5 males entered into the group (4 adults and 1 immature), and 8 immigrant males left the group (7 adults and 1 subadult).

NB: The Sendero group's home range fell within the current LV home range (see LV range on map in Appendix A).

Cerco de Piedra Group (CP):

Observations on the CP group also commenced in 1984 with complete differentiation between adult individuals occurring by 1986. In June 1986 the group was comprised of 23 individuals, including 7 adult males, 6 adult females, 1 large immature male, 1 large immature female, 5 small immatures (unsexed), and 3 infants (unsexed). All 7 of the adult males and the one large immature male have been included in our sample of immigrant males. The data used in the following analyses makes use of the complete fourteen years of behavioral and demographic data collected on the members of the CP group from June 1986 through May 2000. During this period 13 males entered into the group (7 adults, 2 subadults, and 4 immatures) and 18 males left the group (13 adults; 2 subadults, and 3 immatures) including one adult male who was killed during a group takeover.

Los Valles Group (LV):

The Los Valles group was added to the long-term study groups in 1990 after several members of the CP and SE groups immigrated into it. The group continues to be the focus of intensive study to this day. When observations of the group began, there were 18 members present: 3 adult males, 2 subadult males, 4 adult females, 4 large immature males, 1 small immature female, and 4 independent infants (2 males; 2 females). All 3 of the adult males and the 4 large immature males are included in our sample of immigrant males. One of the large immature males was known to have previously emigrated from the neighboring SE study group, and the other three were also suspected to be immigrants given their estimated ages when the study began in 1990 ($\geq$ 5 years).

Bosque Humedo (BH), Cuajiniquil (CU), and Cafetal (CA) Groups

In Dec. 1996, 8 males disappeared from the LV group, including two immigrant adult males, 3 subadult males (1 immigrant; 2 natal), and 3 large immature natal males. These males were located in January 1997 and they had taken over the CU and BH groups to the north of the LV

range (see map in Appendix A). These two groups were observed intermittently between January and June 1997, continuously from Jan. 1998 through June 1999, and then monitored bi-monthly until Sept. 1999. As of June 1999, all of the then-subadult males had emigrated from the two groups, and all but two had been located in their new groups. The BH group was last observed in Feb. 2000 and only one adult LV male remained in the group (same composition as June – Sept. 1999). The CU group no longer contained any of the previous LV males due to the independent immigration of the two former CU males into the neighboring Cafetal group (their immigrations were separated by 6.5 months). While in Cafetal (CA), these two former SE natal/LV immigrant/CU immigrant males were observed continuously for a two month period in 1999. The BH and CU males are only used in the analyses where specified.

Data Analysis

SPSS SURVIVAL analysis was used to determine the length of male tenure in the study groups. This analysis allows for the use of both completed/uncensored intervals (known male tenure within groups), and incomplete/uncensored intervals (i.e. males who were present in groups when the study began, or males that remained in the groups in May 2000). This method of analysis is preferred as analysis based solely on complete intervals often results in shorter intervals. SPSS-SURVIVAL analysis generates the median survivorship for each group (tenure length in this study) and performs a Wilcoxon (Gehan) test for comparing survival distributions between groups. A Wilcoxon Signed Ranks test is used to compare the sex ratios of the groups males transferred between, and the rank of these males before and after their transfer between known groups. Binomial tests are also used where specified. Significance was set at $p \leq 0.05$ (two-tailed probabilities) for all statistical analyses.

RESULTS

Types of immigration

Table 3.1 summarizes the details surrounding the immigrations of the 34 males (19 adults, 4 subadults, and 11 immatures) who entered into the three main study groups (SE, CP, LV) during the specified periods. One immature male was excluded from the analysis as he entered during a period of researcher absence. Note, that the sample of immature males moving into the study groups does include several males known to be dispersing directly from their natal groups, and it is likely that many of the immature males were immigrating for the first time. These males are included here to allow for a comparison of immigration styles between the three age-classes. All subadult and adult males entering the groups were considered secondary immigrants, as we have never observed a male to remain in his natal group past 8 years (Chapter 2).

Thirteen of the 33 males, or 39% of the immigrant sample, entered into the groups by taking over group leadership. All 13 of the males involved in group takeovers were adults and they represent 68% of the immigrant adult males in the sample. It is important to note, however, that researchers in SRNP have observed or inferred takeovers in non-study groups in which subadult and even immature males were involved, although the participation of these young males was minor (e.g. facial threats). The 13 males involved in group takeovers represent only seven actual takeover events. Of these, three were carried out by single males, while the others involved the cooperation of two or more males (see Table 3.2 for details). Of the three takeovers by solitary adult males, two were into groups containing only a single resident male and one of these attempts was unsuccessful, and the third single male takeover was directed at a group with one adult and one subadult male. Following this latter takeover, the two resident males remained in the group with the invader male as the new alpha. With the exception of one other instance where a former alpha male remained in the LV group for four months following a takeover, all other resident males were evicted from their groups.

We cannot be certain that we didn't miss other unsuccessful takeover attempts. Members of the SRNP research team have frequently observed several males "checking out" the study groups, possibly with the intent of taking over, or joining peacefully. However, these males were always chased away by the resident males before any overt takeover attempts began. Rose (1998) details the unsuccessful takeover attempt of the LV group by a single male (Side). After being evicted from his own group by several former LV males, Side tried to move into LV, which at the time had only one resident male, Butch. Although Butch was badly wounded in the takeover attempt, the LV females supported him (groomed him, formed coalitions with him against Side, and followed Butch rather than Side) and he was able to remain in the group as the alpha male, at least for a while. Side eventually joined the group as a subordinate following the takeover of LV by two neighboring males.

A higher percentage of males, 61%, entered the study groups in an unobtrusive fashion (N=20; 6 adults, 4 subadults, 10 immatures). Ten of these 20 males did so on their own while the remaining ten males entered in the company of other males. With one exception, all of the adult males who entered groups unobtrusively joined groups that did not contain resident males (i.e. the resident males were absent or had already dispersed). The exception involved the male Nose who was the CP alpha male. He transferred into LV shortly after his two subordinate coresident males had aggressively taken over the group. Nose just moved into LV and assumed the role of alpha male, his former coresident males giving way, and he was not challenged as alpha male for many months (Rose, 1998). The unobtrusive entry of a single adult male into a group, joining the group's resident males, and assuming a low ranking position within the new group, has never been observed in the Santa Rosa study groups.

Male tenure within groups

The tenure of immigrant males residing within the study groups was calculated for a total of 61 males: 41 individual immigrants, 12 of whom moved between study groups (i.e. males were

residents in more that one of our groups), and 8 males who transferred into the two newest groups, BH and CU. The exact length of tenure for 24 of these immigrant males is unknown as several were present in the groups when observations began, and others were still residing in the groups as of May 2000. These cases have been assigned censored (incomplete) intervals to their tenure data. SURVIVAL analysis showed that median tenure for all of the 61 males was 40.97 months and ranged from 4 to 67 months. Data were then compared for differences between the three age classes (adult, subadult, immature), with each male labeled as a member of the age class he belonged to when he was first observed. For example, if a male entered into a study group as an immature and left as a subadult, he was classified for this analysis as an immature. According to SURVIVAL analysis the median tenure for adult males was 48.94 months (N=32), subadults 27.67 months (N=10), and immatures 42.71 months (N=19). Adult males had significantly longer tenure within groups than subadult males (Wilcoxon Gehan = 6.186, p=.01), while the other age class comparisons did not yield significant differences. This indicates that "survivorship", defined as tenure length, is predicted by the age class of the subject.

Proximate cause of emigration and frequency of parallel dispersal

A total of 54 emigration events occurred during the specified periods for the five study groups. Three of these events were not included in this analysis, because two occurred during a period of researcher absence and the third involved an adult male who was suspected to have died. The circumstances surrounding the remaining 51 departures from the study groups were examined according to male age class (33 adults; 10 subadults; 8 immatures) and labeled according to whether they appeared voluntary or were the direct result of eviction from the group following a takeover by new immigrants. The emigration events were further divided according to whether the males dispersed in the company of coresident males, into groups containing familiar males, with non-male group members, or if they dispersed on their own. Forty-five of the 51 observed emigrations appeared to be voluntary, and all of the subadult and immature males

dispersed from their groups in this manner (Table 3.3). Eighty-two percent of the adult males in our sample (N=27) also dispersed from the groups under what appeared to be voluntary circumstances. Only six males in the sample dispersed due to eviction from the group and all of these cases involved adult males (Table 3.4).

Caution is warranted in the interpretation of these results, however, as all emigrations that did not occur in the context of a group take-over, or following the entry of new males in the group, were labeled as "voluntary". We are not necessarily implying that the dispersing males were not the recipients of aggression by coresidents prior to their departure. The exchange of aggression between coresident males is normally quite low (Fedigan, 1993; Chapter 5), however, there have been instances where aggression between coresident males may have in fact prompted the subsequent dispersal of group males (Rose, 1998; see also Perry, 1998). There were also several instances where a takeover may have occurred during times when daily observations were not made. In these cases it appeared more likely that the resident males had dispersed prior to the arrival of the new males as the immigrants exhibited no visible wounds, a characteristic of aggressive takeovers and the eviction of resident males (but see Rose, 1998).

The frequency of parallel dispersal, that is dispersal with coresident males or into groups containing familiar males, was very high in our sample. Table 3.5 summarizes the frequency of parallel dispersal for each age class. Of the 51 emigrations, 36 (71%) were parallel and two additional males dispersed in the company of other coresidents (adult females and infants). Excluding those migrations with non-male coresidents, the rates of parallel emigration according to male age class were: 67% for adult males (N=22), 80% for subadult males (N=8), and 75% for immatures (N=6). Several of these dispersing males were subsequently observed in their new groups and 19 of these (9 adults; 5 subadults; 5 immatures) were confirmed as parallel transfers.

Season/month of male migrations

Male migrations (both immigrations and emigrations) were separated by age class and according to the month in which they occurred. Those males who were either confirmed or strongly suspected to have died rather than emigrated were excluded (N=2) and those males who moved between study groups were only counted once as transfers between groups usually occurred within the same month. Males for whom the exact month of departure could not be pinpointed due to a period of researcher absence (N=6), were divided across the range of months during which their emigration possibly occurred. For example, if two males disappeared during the four month period between August and November when monthly observations were not made, 0.5 migrations were recorded occurring during each of those months. These males were included to avoid sampling bias because the periods of researcher absence usually coincided with the rainy season.

In total, 67 migrations involving 41 adult, 8 subadult, and 18 immature males were examined. Seventy-six percent (N=51.5) of the migrations took place in the dry season (Dec. through May) and 24% (N=15.5) occurred during the wet season (June through Nov.) (see Figure 3.1). This seasonal difference was significant (Binomial test, $p<.000$). Data were also examined according to male age class. Adult and subadult migrations were mainly confined to the dry season, 86% and 92% respectively, while the migration of immatures was evenly spread between the two seasons. The seasonal difference observed in adult male migrations was significant (Binomial test, $p=.000$), while that of subadult males migration was not (the non-significant result was a function of the small sample size as 7 of 8 emigrations occurred in dry season).

Group transfers by adults and subadults: changes in rank and sex ratio

Eleven males (8 adults and 3 subadults) moved between our three long term study groups and five males (4 adults and 1 subadult) moved into non-study groups where observations began after their transfers. One immature individual also moved between groups, but is not included in this

analysis because his rank was unknown. I compared the rank of males in their groups before and after their transfer, and no males in our sample (N=16) experienced a decrease in their rank; four retained the same rank and twelve increased their rank by at least one position. The increase in male rank after their transfer was significant (Wilcoxon signed ranks test: Z=-3.082, p=.002). All 16 of these males transferred into groups with a lower ratio sex ratio (male to females) and this change was also significant (Z=-3.523, p=.000).

It is interesting to note that with the exception of one of these transfers, all were voluntary dispersals rather than the result of eviction from their former groups. This may indicate that evicted males are experiencing higher mortality than those transferring voluntarily. However, several of the evicted males have been observed in more distant groups over the years, but unfortunately we lack the comparative information (sex ratio and rank) for these groups that comes only through intensive observations. Also, in many cases these "missing" males are not seen for several years following their disappearance, and in some cases there was a five year period separating the events. It is quite likely then, given male tenure within groups of white-faced capuchins, that these males have dispersed several times since they left our study groups.

DISCUSSION

My main goal in this paper was to address the effect of varying life history stages on the migration patterns of non-natal male white-faced capuchins. First, I examined the patterns of male immigration observed within the Santa Rosa National Park (SRNP) study population. Previous accounts of male immigration in white-faced capuchins indicated that they enter into groups in one of two ways: they immigrate alone into a group, joining resident males (Perry, 1996), or they cooperatively and aggressively enter a group and evict resident males (Fedigan, 1993). In our study population, the way males enter social groups differed according to age class. Although males of all ages are able to enter groups in an unobtrusive, peaceful fashion, unless they are in the company of adult males, physically immature males (subadults and immatures) are

restricted to entering groups in this manner. Adult males, on the other hand, appear to have a choice: they may enter a group aggressively, evicting resident males, or they may enter unobtrusively.

The majority of adult males in our sample chose the aggressive option, although these takeovers were not always cooperative in nature as has been previously reported for this species (Fedigan, 1993). Several of the group takeovers our research team has observed over the years involved a single adult male aggressively entering a social group and taking over as the group's dominant male. All takeovers brought about by a single male involved a target group that contained only one resident adult male. It was also very interesting to find that in our sample of adult males entering groups unobtrusively, not one of them actually joined a group containing resident male(s). In all of these peaceful immigrations, the new males did not display any overt wounding and they appeared to enter groups opportunistically when resident males were either away from the group or had previously dispersed.

During the course of my fieldwork, I observed simultaneous changes in male membership within two neighboring groups and these clearly illustrate the methods of adult male immigration as described above. Also, because the two events were linked, they demonstrate how one event can invariably lead to the other; this may explain the simultaneous takeovers observed several times in our long term study groups. Although the entire sequence of events was not directly observed, my assistants and I saw enough of the prelude, the events themselves, and the aftermath that I am able to construct the following summary.

In mid May 1998 Garth, who was the beta male (9 year old subadult) of the Cuajiniquil group, disappeared leaving the alpha male, Spike (an 11 year old and his probable maternal sibling), as the sole resident of the group. Garth was observed three months later as a member of the neighboring Cafetal group. On several occasions between September and December 1999 Spike "visited" the Cafetal group, usually in the aftermath of an intergroup encounter. Spike's visits in Cafetal were mostly peaceful with only minor threats and displays received from some

Cafetal group members. His presence in the group was likely tolerated due to his familiarity not only with Garth but with the group's alpha male, Sundance. Sundance was also a former member of the LV group in which both Spike and Garth had resided for over 5 years, and they were well known to each other. By January 1999, it appeared that Spike was trying to enter into the Cafetal group. He began disappearing from his group more frequently and he displayed some minor wounds (as did Sundance); on one occasion Spike was found on the periphery of the Cafetal group, being vigorously courted by four of the group's adult females, one of whom followed him back to his own range that evening. Although no direct fighting between the males was observed, towards the end of January both Spike and Sundance bore more severe wounds. Interactions between the two males became noticeably more tense and threats were frequently exchanged. It also became evident that Spike was being supported by several of the group's older females, while Sundance seemed to retain the support of the group's younger males. Garth remained uninvolved in these initial conflicts between Spike and Sundance, and chose instead to direct his threats towards the human observers.

At the same time as Spike's visits to Cafetal became more frequent, one adult and two subadult males were spotted together in the area. Although their entrance into the Cuajiniquil group was not observed, it appeared that these three males moved into the group with complete ease when Spike was absent from the group as none of them displayed so much as a scratch. I observed Spike being chased from the Cuajiniquil group on one occasion, and he retreated without a fight; he was no match for three males. Instead, Spike returned to Cafetal and fought it out with Sundance. With Garth's support, Spike emerged as the victor. After the takeover, all three males displayed wounds, although Garth's were very minor and probably indicative of the role he played. Sundance had deep canine slashes across the back of his right thigh and across each shoulder, while Spike came out of the fight with a new smile: a large piece of flesh had been torn from his upper lip permanently exposing his upper right canine.

The above scenario most clearly illustrates the opportunistic nature of adult male immigration in white-faced capuchins. It also demonstrates the importance of female support and male coalitions, and the benefits of parallel emigration. It is probable that the ways individual adult males enter groups change as they age: Spike was a 12 year old male in his prime and it is doubtful that he could withstand (and win) fights of this nature throughout his life. Van Noordwijk and van Schaik (1985) found that among male long-tailed macaques, it was only young adult males, the age when males have greatest fighting prowess, who entered groups in an aggressive fashion. This may also be the case for white-faced capuchins, as all of the males involved in aggressive group takeovers have been described as being in their prime. However, additional data are needed before conclusions can be reached as observations of "old" adult males in our study groups, and in the population as a whole, are relatively infrequent.

The maximum life span of male white-faced capuchins in SRNP is currently unknown; however, the oldest males observed in our study groups have been estimated to be at least 18 years of age. At 18 years, these males were not "old" looking, as other males in our study groups and park-wide censuses have been described, and it is likely that males do live well beyond this age. The life span of white-faced capuchins in captivity has been reported to be as long as 46.9 years (Ross, 1991, c.f. Rowe, 1996), but given the short tenure of males within groups in the wild (see below), and the often violent nature of male migrations, it is doubtful that they would ever reach this age.

The length of male tenure within groups of white-faced capuchins is relatively short, averaging just under 3.5 years over all ages (immigrants). Of the three age classes, adult males had the longest tenure within groups and this is likely because adult males are most at risk of harm during dispersal than are younger males. The data reviewed in this study demonstrate that immature and subadult males only enter groups peacefully, unless in the company of more aggressive, physically mature males. These adult males, on the other hand, are more often the

recipients of conspecific aggression and this aggression can be lethal indicating that adult males likely benefit the most from longer tenure within groups.

Why then do we see so many instances, like those described above for Spike, where resident males go wandering off to "visit" other groups? It is curious that dispersal, which is inevitably rife with risks (predation, aggression from conspecifics, lack of food), would occur so frequently. It has been suggested that the frequent dispersal of male white-faced capuchins in SRNP is linked to the large number of males in the population due to male-biased infant sex ratios (Fedigan *et al.*, 1996). But the majority of the secondary dispersals observed appear to be voluntary in nature. Ultimately, male dispersal is presumed to be a means of increasing reproductive success (Alberts & Altmann, 1995), but what are the proximate reasons for male secondary dispersal? Are these immigrant males also attracted to extragroup males and dispersing group mates, as was the case for dispersing natal males (see Chapter 2), or are they attracted to extragroup mates?

Similar to natal dispersal, eviction as a proximate cause of secondary emigration was infrequent for adult males (only 18% of our sample) and was not an issue for either subadults or immatures. The high frequency of parallel emigration among male white-faced capuchins of all ages may indicate that males are dispersing in response to an attraction to extragroup males or to dispersing group mates. In other species where males migrate in the company of group mates, it is much more commonly observed among young males than among adults (see Pusey & Packer, 1986 for review). This was not the case in our sample of males as parallel dispersal remained high for all age classes; natal males 71%, immatures, 75%, subadults 80%, and adults 66%. The slightly lower rate of our confirmed cases of parallel dispersal among adult males may indicate that, like several cercopithecine species, adult male white-faced capuchins are dispersing greater distances than are younger males (Cheney & Seyfarth, 1983; Pusey & Packer, 1986). If this is the case, members of our research team would be less likely to encounter these males. In fact, during our park-wide censuses, several familiar males have been located in distant groups, some of which had not been observed for many years. Several younger males have also been observed

immigrating into groups previously unfamiliar to our research team, and some of these groups contain familiar adult males that disappeared from our study groups up to five years previous.

These examples, coupled with the high frequency of parallel migration, provide strong evidence for the argument that males are dispersing in response to an attraction to familiar extragroup males and/or dispersing group mates. However, our observations that both adult and subadult males are also transferring into groups with more favorable sex ratios, indicate that there is also an attraction to extragroup mates. The majority of transferring males also experienced an increase in their ranks. However, until we determine if high dominance rank confers a reproductive advantage, we cannot conclude that males are attempting to increase their ranks in an attempt to increase their access to mates. It is likely that both of these factors are influencing male migration patterns, and that parallel dispersal facilitates male immigration by providing immigrating males with known allies within the new group (Cheney & Seyfarth, 1983; van Noordwijk & van Schaik, 1985; van Hooff, 2000).

The seasonal pattern observed in the dispersal of adult males, and to some extent subadults, confuses the issue somewhat. If males are dispersing due to an attraction to extragroup mates, I predicted that the majority of migrations would be occurring during, or just prior to, the "conception peak". However, the pattern that has emerged from our analysis of the SRNP data demonstrates that significantly more migrations occur during the birth peak (dry season) than the conception peak (rainy season). It is possible that males may be joining a group prior to the "conception peak" because they experience a lag between membership in a new group and successful mating access to females. However, our observations of new males mating shortly after joining a new group make this an unlikely scenario (pers. obs.). Another possible explanation for this seasonal pattern of dispersal, is the frequency of intergroup interactions that occur in SRNP during the dry season when several groups share access to the few permanent water holes. Threats and displays are frequently exchanged between the males of the opposing groups (females often flee during such encounters; Perry, 1996; pers. obs. KMJ), but in this

context, the events rarely escalate to contact aggression. Instead, they usually end with the smaller group retreating and returning to the water source after the larger group has left the area (KMJ unpublished data).

Perry (1996) suggests that such non-aggressive encounters between groups enable males to become familiar with each other and assess the possibilities of transferring into the group in the future. Such encounters may also provide males with the opportunity to observe the number, presence, or physical state of competitors within neighboring groups, and to determine whether familiar males who may serve as future allies are present in the group. Group transfer following intergroup interactions was a common circumstance surrounding male natal emigration in white-faced capuchins (see Chapter 2), and intergroup interactions may very well influence male transfer at other stages in their life history.

It is also possible, however, that this pattern of dry season (birth peak) dispersal, reflects an evolved reproductive strategy; that is, males may preferentially disperse during the birth peak as this timing would enable them to manipulate female reproduction in the new groups that they enter. Fedigan *et al.* (1996) reported that 58% of the infant deaths in the SRNP study population were concurrent with new males entering into groups, and this may be a strategy employed by males to increase their own reproductive potential within new groups (see Hrdy, 1976). Male dispersal during the dry season is a pattern that seems to be firmly in place by the time a male reaches the subadult stage of his life. However, we have never observed a subadult male wounding, let alone killing, an infant, which questions the validity of this argument of seasonal dispersal as a reproductive strategy. This said, I am not ruling out the argument of male manipulation of female reproduction as a possibility, but it is beyond the scope of this paper. It does merit future investigation, particularly in light of genetic confirmation of male reproductive success within groups which is currently in preparation. For the present, however, observations indicate that male secondary dispersal, particularly among adult and subadult males, is due to an attraction to extragroup mates regardless of a male's ability or intent to interfere with female

reproduction. Males may preferentially disperse with group mates, or enter into groups containing familiar males, to decrease the costs of dispersal, but the frequent voluntary dispersal in this species does appear to be an attempt to maximize reproductive opportunities, and ultimately reproductive success.

Life history of male white-faced capuchins

Although we do not have a complete life history on any of the males in the Santa Rosa population, by combining the data for males at varying ages, a picture of the "average" life of a male white-faced capuchin can be devised. At 4.5 years of age, a male voluntarily leaves his birth group, often in the company of maternal kin or members of his age cohort, and transfers unobtrusively into a neighboring group. This natal transfer is likely to take place during the dry season following a series of intergroup interactions in the vicinity of a waterhole. The male spends the next 3.5 years as a resident of this second group and at around 8 years of age the now-subadult male transfers again, unobtrusively and usually in the company of group mates or into a nearby group containing familiar males. Now in his third group, the male remains until he is approximately 10.5 years old and has reached full physical maturity. It is at this time that he disperses for a third time, perhaps in the company of group mates, and most often during the dry season. But this time the male must either fight his way into a group, or find a group that has been deserted by its resident male(s). The male is now in his fourth group and perhaps he is the alpha. If he is lucky, he will remain in the group for the next four years, until he is either evicted by immigrating males or he himself goes wandering off in search of a new group with greater reproductive opportunities.

This picture that comes out of the analysis of the long term data at SRNP is almost identical to the life history of Spike, whom I have previously referred to above. Spike has been observed longer than any other male in the Santa Rosa study population. He was born into the Sendero group in 1987 and transferred into the Los Valles study group at the age of 4 years 3 months. His

natal dispersal was parallel; he left in the company of a younger coresident male following a series of intergroup interactions during the dry season, and these males were joined one month later by Garth, whom we strongly believe is Spike's younger maternal sibling. Spike remained in Los Valles until he was 9 years 10 month of age, at which time all of the LV males, with the exception of the alpha, dispersed from the group. Exactly what happened either before or after the initial dispersal of the LV coresident males is unknown, as all members of the Santa Rosa research team were absent from the park for a period of 5 months. However, when a member of the team returned, Spike was the alpha male of the small Cuajiniquil group and Garth was his beta male. After a year and a half in the Cuajiniquil group Garth transferred into the neighboring Cafetal group, and Spike followed 6 months later, aggressively taking over as the group's alpha male. However, Spike's tenure in this fourth group, was short lived. After only three months he lost his alpha position and Garth emerged as the alpha male with the assistance of the group's former alpha male, Sundance. Spike was last observed looking very healthy and moving through the range of an adjacent group, perhaps assessing his possibilities.

Table 3.1 Number of males and age class according to type of immigration.

Type of immigration	Adult	Subadult	Immature	Total
aggressive takeover	13	0	0	13
unobtrusive	6	4	10	20
unknown	0	0	1	1
Total	19	4	11	34

Table 3.2 Details of male takeovers

Number of invaders	source group – target group	# resident males in target/evicted?	Success of takeover attempt*
4 adults (Right, Diablo, Pirate, Nose)	? – CP	2 adults/yes	yes
2 adults (Diablo, Pirate)	CP – LV	1 adult/after 4 months	no: former CP alpha (Nose), unobtrusively takes over after 1 month
2 adults (Lea; Perrins)	? – LV	2 adults/alpha evicted beta remains	yes
2 adults	? – SE	1 adult/yes	yes
1 adult male (Churchill)	? – CP	1 adult, 1 subadult/both remain as subordinates	yes
1 adult (Steptoe)	LV – SE	1 adult/yes	yes
1 adult (Side)	? – LV	1 adult/no	no/eventually joins as subordinate

*A takeover was considered successful if the invading males remained in the group and assumed the top ranking position(s) in the male hierarchy.

Table 3.3 Summary of male voluntary emigration.

	Adult	Subadult	Immature	Total
With coresident males	18	6	3	27
Joins familiar male(s)[a]	3	2	3	8
With non-male coresidents	1	0	1	2
Alone	5	2	1	8
Total	27	10	8	45

a. dispersing male enters into a group containing a familiar male

Table 3.4 Summary of male emigration by eviction.

	Adult	Subadult	Immature	Total
With coresident males	0	0	0	0
Joins familiar male(s)[a]	1[b]	0	0	1
With non-male coresidents	0	0	0	0
Alone	5	0	0	5
Total	6	0	0	6

a. dispersing male enters into a group containing a familiar male

b. male returned to his previous group; only adult females and immatures were present

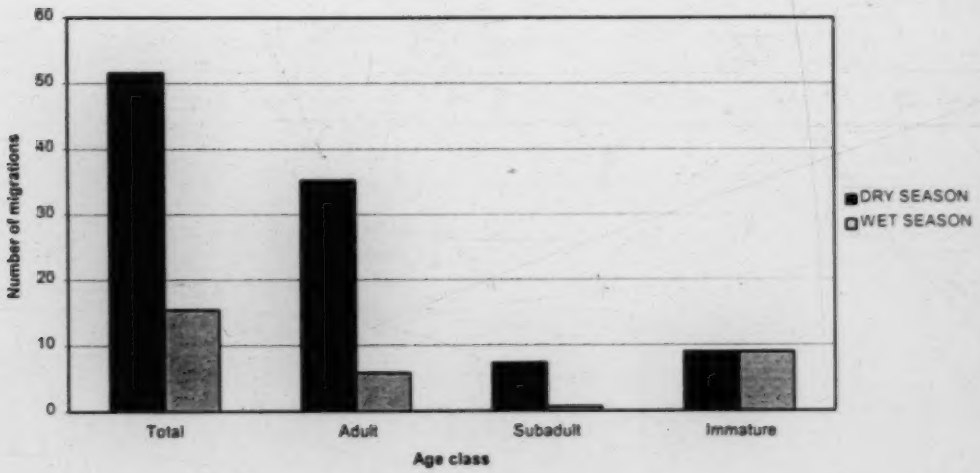
Table 3.5 Frequency of male parallel dispersal according to age class.

	Adult	Subadult	Immature	Total
Parallel*	22 (67%)	8 (80%)	6 (67%)	36 (71%)
With non-male coresident	1	0	1	2
Alone	10	2	1	17
Total	33	10	8	51
Confirmed parallel*	9 (26%)	5 (50%)	5 (56%)	19 (37%)

NB. Excludes two adult males that died

* percentages given are for the total number of males in each age class

Figure 3.1 Seasonal patterns of male migration according to age class.



REFERENCES

Alberts, S.C. and Altmann, J. 1995. Balancing costs and opportunities: Dispersal in male baboons. *Amer. Naturalist*, 145:279-306.

Alberts, S.C., Sapolsky, R.M., and Altmann, J. 1992. Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate groups. *Hormones and Behav.*, 26:167-178.

Altmann, S.A. and Altmann, J. 1970. *Baboon Ecology*. University of Chicago Press, Chicago.

Chapman, C., Fedigan, L.M. and Fedigan, L. (1988). A comparison of transect methods of estimating population density of Costa Rican primates. *Brenesia*, 30: 67-80.

Cheney, D.L. and Seyfarth, R.M. 1983. Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *Amer. Naturalist*, 122:392-412.

Fedigan, L.M. 1986. Demographic trends in the *Alouatta palliata* and *Cebus capucinus* populations of Santa Rosa National Park. In: *Primate Ecology and Conservation*, Vol. 2 Else, J.G. and Lee, P.C. eds. pp.287-93. Cambridge: Cambridge Univ. Press.

Fedigan, L.M. 1993. Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol.*, 14: 853-877.

Fedigan, L.M., Fedigan, L. and Chapman, C.A. 1985. A census of *Alouatta palliata* and *Cebus capucinus* in Santa Rosa National Park, Costa Rica. *Brenesia*, 23: 309-22.

Fedigan, L.M. and Rose, L.M. 1995. Interbirth interval variation in three sympatric species of neotropical monkey. *Amer. J. Primatol.*, 37:9-24.

Fedigan, L.M., Rose, L.M. and Avila, R.M. 1996. See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In: *Adaptive Radiations of Neotropical Primates* (M. Norconk, A. Rosenberger & P. Garber, eds.) Plenum Press, New York, p.289-308.

Fedigan, L.M. and Jack, K.M. in press 2001. Neotropical primates in a regenerating Costa Rican dry forest: A comparison of howler and capuchin population patterns. *Int. J. Primatol*, 22(5): 689-713.

Fragaszy, D., Fedigan, L.M. and Visalberghi, E. (in prep.). Social behavior: Interaction, relationships and social structure. In: *The Complete Capuchin Monkey*. Cambridge University Press, Cambridge.

Henzi, S.P. and Lucas, J.W. 1980. Observations on the intertroop movement of adult vervet monkeys (*Cercopithecus aethiops*). *Folia Primatol.*, 33:220-235.

van Hooff, J.A.R.A.M. 2000. Relationships among non-human primate males: a deductive framework. In: *Primate Males: causes and consequences of variation in group composition*, (P.M. Kappeler, ed.) Cambridge University Press, Cambridge, p.183-191.

Hrdy, S.B. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Advanc. Study Behav.*, 6:101-158.

Hrdy, S.B. 1977. *The langurs of Abu*. Harvard University Press, Cambridge.

Itani, J. 1972. A preliminary essay on the relationships between social organization and incest avoidance in non-human primates. In: *Primate Socialization*. New York: Random House, pp. 165-171.

Janzen, D.H. and Hallwachs, W. 1995. Indicative weather data for the Santa Rosa area and Volcan Cacao. Unpublished ms.

Manson, J.H., Perry, S. & Parish, A.R. 1997. Nonconceptive behavior in bonobos and capuchins. *Int J. Primatol.*, 18:767-786.

Melnick, D.J. and Pearl, M.C.1987. Cercopithecines in multimale groups: genetic diversity and population structure. In: *Primate Societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.) University of Chicago, Chicago, pp. 121-134.

van Noordwijk, M.A. and van Schaik, C.P. 1985. Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). *Anim. Behav.*, 33:849-861.

Packer, C. 1979. Intertroop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.*, 27:1-36.

Perry, S.E. 1996. Intergroup encounters in wild white-faced capuchin monkeys, *Cebus capucinus*. *Int. J. Primatol.*, 17: 309-330.

Perry, S.E. 1998. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behav.*, 135: 139-172.

Pusey, A. E. and Packer, C. 1987. Dispersal and philopatry. In: *Primate Societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.) University of Chicago, Chicago, pp. 250-266.

Rose, L.M. 1998. *Behavioral ecology of white-faced capuchins (Cebus capucinus) in Costa Rica.* Ph.D. dissertation, Washington University-St. Louis MI, University Microfilms International.

Ross, C. 1991. Life history pattern of New World monkeys. *Int. J. Primatol.*, 12(5):481-502.

Sprague, J.S. 1992. Life history and male intertroop mobility in Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.*, 13:437-454.

Sprague, D.S., Suzuki, S, Takahashi, H., and Sato, S. 1998. Male life history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. *Primates*, 39:351-363.

Strier, K.B. 2000a. *Primate Behavioral Ecology*. Allyn & Bacon, MA.

Strier, K.B. 2000b. From binding brotherhoods to short-term sovereignty. In: *Primate Males: causes and consequences of variation in group composition*, (P.M. Kappeler, ed.) Cambridge University Press, Cambridge, p.73-83.

Strier, K.B. 1999. Why is female kin bonding so rare? Comparative sociality of neotropical primates. In: *Comparative Primate Socioecology*, P.C. Lee (ed.), Cambridge University Press, Cambridge.

Sugiyama, Y. 1976. Life history of male Japanese monkeys. In: *Advances in the Study of Behavior, Vol. 7* (Rosenblatt, J.S. ed.) Academic Press, New York, pp.255-284.

Sugiyama, Y. and Ohasawa, H. 1975. Life history of male Japanese macaques at Ryozenyama. In: *Contemporary primatology: Proceedings of the Fifth Congress of the International Primatological Society*, ed. S. Kondo, M. Kawai, and A. Ehara. Basel: S. Karger.

Sussman, R.W. 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *Int. J. Primatol.*, 13:395-413

CHAPTER FOUR

Effect of male emigration on the vigilance behavior of coresident males in white-faced capuchins (*Cebus capucinus*)

INTRODUCTION

Primates display an almost universal pattern of gregariousness, with the vast majority of species residing in stable groups containing multiple males and females (Smuts *et al.*, 1987). Attempts to explain the adaptive significance and evolution of group living and group composition have been numerous (e.g. van Schaik, 1983; O'Brien, 1991; Rose, 1994a; Treves & Chapman, 1996) and attention has recently turned to explaining the number of males in primate groups (e.g. Mitani *et al.*, 1996; van Schaik, 1996; Pereira, 1998; Nunn, 1999; Kappeler, 2000). Mitani *et al.* (1996) tested the two major competing hypotheses proposed to explain the evolution of the multimale social system in primates: (1) breeding seasonality (Ridley, 1986) and (2) female distribution (e.g. Emlen & Oring, 1977; Wrangham, 1980; Terborgh, 1983; Dunbar, 1988; Altmann, 1990).

The breeding seasonality hypothesis proposes that for those species characterized by female mating synchrony, multiple males will be common because male monopolization of mating access is difficult when females come into estrus synchronously and for relatively short periods (Mitani *et al.*, 1996). The female distribution hypothesis for the evolution of multimale groups proposes that a male's ability to monopolize mating access is dependent upon the spatial distribution of females. Those species with large female group size usually contain multiple males, while those with small female group size contain fewer males. Based on their investigation, Mitani *et al.* (1997) concluded that female group size and consequently, male mating competition (female distribution hypothesis), are the main factors influencing the number of males in primate groups.

There were several exceptions, however, where counter to what is predicted by the above hypotheses, a number of species displayed small female group size but nevertheless exhibited a

multimale social system (Mitani *et al.*, 1996). White-faced capuchins (*Cebus capucinus*) were among these exceptions as they are not seasonal breeders (Fedigan *et al.*, 1997) and their average group composition is 5.5 adult males and 4 adult females (Mitani *et al.*, 1996 from Fedigan, 1993). Explaining the existence of the capuchin multimale-multifemale social system presents a particularly challenging problem. Mitani *et al.* (1996:326) suggest that group composition for those species that cannot be explained by female defensibility and male mating competition may be attributed to "the benefits gained by males who tolerate others [males] in groups". The potential benefits that males may gain include: decreased predation risk, cooperation against extragroup conspecifics, and increased reproductive success of related coresident males (Mitani *et al.*, 1996).

White-faced capuchins reside in groups containing related females, their offspring, and what are thought to be unrelated immigrant males (Oppenheimer, 1968; Freese, 1978; Fedigan, 1993). Male white-faced capuchins have been observed to emigrate together or to disperse into groups that older, familiar males have previously joined and the rates of such parallel dispersal do not decrease with male age (Chapter 2; Chapter 3). However, until there is concrete evidence on the genetic relationships of coresident males, we cannot be certain that an increase in the reproductive success of related coresidents is a benefit secured by male white-faced capuchins. Regardless of the presence or absence of kinship among males in this species, the cooperation of group males during encounters with predators and extragroup conspecifics is crucial in protecting the group and retaining residency (Rose & Fedigan, 1995; Perry, 1995 ,1996). This added protection from the attacks of predators and/or conspecifics may be the main benefit that the presence of multiple coresident males provide to both female and male members of their group.

Since researchers are unlikely to observe predator-prey interactions and intergroup encounters often enough to allow for the testing of relevant hypotheses, many investigators have looked at vigilance behavior as an indicator of the severity of these threats (e.g. Baldellou & Henzi, 1992; van Schaik & Höstermann, 1994; Blumstein, 1996; Treves & Chapman, 1996;

Treves, 1997, 1999). However, in addition to vigilance directed at detecting predators and conspecifics, group living individuals may also direct vigilance against members of their own group (social monitoring hypothesis: Kervene *et al.*, 1978; Caine and Marra, 1988). According to Caine and Marra (1988), in those species with rigid dominance hierarchies, individuals will engage in high levels of social vigilance at a cost to vigilance directed at detecting threats external to the group (non-social vigilance). When this occurs, it is beneficial to increase group size, particularly in the sex that is most active in detecting and defending against predators and conspecifics, as the costs of social vigilance will decrease when there are more individuals present to monitor the nonsocial environment.

Among all four species of capuchins, males are significantly more vigilant than females (Robinson, 1988a, 1988b; van Schaik & van Noordwijk, 1989; Fragaszy, 1990; Fedigan, 1993; Rose, 1994a, Rose & Fedigan, 1995). In *Cebus capucinus*, *C. albifrons* and *C. apella*, it is the number of males in a group that influences individual rates of non-social vigilance, rather than the total number of group members (van Schaik and van Noordwijk, 1989; Rose and Fedigan, 1995). That is, the greater number of males in a group the less time individuals of both sexes spend being vigilant towards threats external to the group. This would allow members of groups containing more males to devote an increased amount of time to foraging, resting and engaging in social interactions. Rose and Fedigan (1995) suggest that because both sexes benefit from male non-social vigilance, this behavior may have been an important factor in the evolution of the multimale social system in *Cebus capucinus*. Non-social vigilance may then be a good indicator of the benefits males receive by tolerating the presence of coresident males: protection for themselves, their mates, and their offspring from predator and conspecific attack (see also van Schaik and van Noordwijk, 1989).

In this paper I examine the vigilance behavior, both social and non-social, of male white-faced capuchins residing in four social groups in Santa Rosa Park, Costa Rica. During the study period, several males emigrated from their social groups, providing ideal experimental conditions

for testing the suggestion put forth by Rose and Fedigan (1995) that male vigilance has been an important factor influencing the evolution of the multimale social system in this species. I address this hypothesis by examining the effect that the emigration of a coresident male had on the vigilance behavior of the males remaining in the study groups. If males are benefiting from the presence of their coresident males in terms of increased protection from predators and/or conspecifics (through their vigilance behavior), I predict that males remaining in their groups will increase their rates of non-social vigilance after the emigration of a coresident male. I will also test Caine and Marra's (1988) suggestion that an increase in social monitoring is a cost of sociality for species with strict dominance hierarchies. If an increase in time spent in social vigilance is a consequence of multiple males within groups of white-faced capuchins, I predict that male social vigilance will decrease after the emigration of a coresident male.

METHODS

Study Site, Species and Subjects

I studied white-faced capuchins (*Cebus capucinus*) in the Santa Rosa Sector of the Area de Conservacion Guanacaste, Costa Rica. Santa Rosa (formerly known as Santa Rosa National Park) lies 35 kilometers northwest of Liberia, in the Guanacaste Province and encompasses approximately 10, 800 ha. of dry deciduous forest and reclaimed pasture. The area experiences two distinct seasons: dry season from December through May, and rainy season from June through November. Annual rainfall in the park averages between 900 and 2,500 mm (Glander *et al.*, 1991). Observational and demographic data have been collected on the white-faced capuchins in Santa Rosa by Dr. Linda Fedigan and her students since 1983.

White-faced capuchins are female-bonded monkeys that range from Panama through Southeastern Belize (Rowe, 1996). They reside in multimale-multifemale social groups thought to contain related females, their offspring, and unrelated immigrant males (Oppenheimer, 1968; Freese, 1978; Fedigan, 1993). Average group size ranges from 11 - 18 individuals with sex ratios

approximating 1:1 (Fedigan *et al.*, 1997). The home ranges of white-faced capuchins are approximately 1 - 2 km^2 (ibid.). On average, males are 25-35% larger than females and they are individually dominant over them (Fedigan, 1993). White-faced capuchins are not seasonal breeders, but they do display a birth peak between January and April (Fedigan *et al.*, 1997). As diurnal forest-dwelling primates, capuchins must anticipate three main types of predators: raptors, felids, as well as constricting and venomous snakes (van Schaik & van Hooff, 1983; Terborgh, 1983). In addition to these three types of predators, the capuchins residing in Santa Rosa must also contend with coyotes and tayras (Freese, 1983; Chapman, 1986).

I studied four groups of white-faced capuchins residing in Santa Rosa from Feb. 1998 through April 1999: Cerco de Piedra, Los Valles , Bosque Humedo and Cuajiniquil (Table 4.1). The Cerco de Piedra group (CP) included two adult males and ranged from 8 - 10 group members during this study. CP was the only study group that did not experience an emigration of a coresident male and is included in this study as a control group. The Los Valles study group (LV) contained three adult males and ranged from 12-15 group members during the time periods compared here (before and after the emigration of a coresident male). An adult male and two immature group members, one 3 year old and one 2 year old, disappeared from LV in late Dec. 1998 or early Jan. 1999 and were not observed again. These three animals disappeared over a 3 week period when the groups were not under observation. The Bosque Humedo group (BH) originally included 1 adult and 3 subadult males. The group totaled 8 members before the emigration of a subadult male in October 1998, who was later observed as a member of a neighboring group. The Cuajiniquil group (CU) was the smallest of the study groups with 2 adult males and a total of 6 group members prior to the coresident male's emigration in June 1998. This young adult male (~ 10 years) was also later observed as a member of a neighboring group.

All members of the four study groups were habituated to the presence of researchers and my assistants and I were able to make observations from 5 – 10 meters. We could individually recognize all individuals residing in the four study groups according to their size, facial

characteristics, and brow shape. Male rank within groups was determined according to the direction of submissive gestures and avoid-supplant interactions observed during focal and *ad libitum* data collection.

Data collection

Three research assistants and I collected data from late February 1998 through April 1999. Prior to the commencement of data collection, my assistants and I practiced together in the field to ensure inter-observer reliability. We collected 1198.25 hours of focal data on all adult males (≥ 10 years) and subadult males (7-10 years) residing in the four study groups. We collected data in 15-minute focal animal continuous-time samples (Altmann, 1974). During these samples we entered all behaviors of the focal male and the identification of interactants directly into a handheld PSION computer using the FOCOBS data entry program designed by Dr. Joan Silk at the University of California, Los Angeles. We collected ten hours of focal observations on all subject males in a group before rotating observations onto the next group. However, due to the inherent difficulty of locating free ranging primates, a strict sampling schedule could not be followed. Efforts were made to sample all individuals for the 10 hour round before moving on to the next study group and to collect no more than two back-to-back samples on any one individual within the study group. We kept records of focal sessions to ensure that each individual was observed equally and at varying times throughout the day. A focal session was discarded if the subject was out of sight for ≥ 2 min. during the 15 min session.

Although the topic of vigilance and its effect on primate grouping patterns has been widely investigated, there is great variation in how this behavior has been defined. For example, Rose and Fedigan (1995:65) defined vigilance as "intently staring beyond immediate vegetation with a stationary, alert posture", while Treves (1998) defined vigilance as scanning beyond arms reach. Cowlishaw (1998) recorded a subject as being vigilant when "its eyes were open and its head up"

while Steenbeek *et al.* (1999) defined it as a head movement of at least 45°. Although this variation no doubt reflects differences between species and conditions under which observations are made, it makes comparisons between study groups and species extremely difficult.

I use two measures of vigilance behavior in this study: social and non-social vigilance. Social vigilance is vigilance directed at events within the group; that is, activities and locations of group members and other non-threatening events in the group's immediate environment (e.g. deer foraging nearby). Non-social vigilance is directed against targets outside of the group, predators and extragroup conspecifics. Although it is difficult to distinguish the exact target of vigilance behavior (e.g. predator vs. conspecific), it is possible, even in a field situation, to distinguish between vigilance directed external to and within the group.

Following Rose and Fedigan (1995), we recorded a focal subject as engaged in non-social vigilance when it ceased an activity and stared beyond the immediate vegetation in an alert, stationary posture. Male non-social vigilance was most commonly recorded before and after the focal animal, group member or another animal species (e.g. agouti, deer, magpie-jay) emitted an alarm call, when sudden loud noises were heard (e.g. branches falling, human shouting), when directing or receiving lost-calls, before and during foraging on the ground and before and during drinking from terrestrial waterholes. This measure of vigilance, therefore, represents the monitoring of events external to the social group and is primarily directed at locating potential predators and/or extragroup conspecifics (Rose & Fedigan, 1995).

We recorded a focal subject as engaged in social vigilance when he interrupted an activity (e.g. foraging, resting, grooming) and scanned beyond the immediate vegetation being watchful of group members or events occurring at close range. This behavior was not accompanied by a distinctive posture, as in non-social vigilance, and was directed around the immediate area occupied by the focal male. Although the behavior was most often directed towards the activities and locations of fellow group members, it was occasionally directed at other non-threatening animals nearby. This measure of vigilance represents an animal's monitoring of the immediate

environment, both social and otherwise. An individual could only be recorded as engaged in one of these behaviors, social or non-social vigilance, at any one time. By separating these two measures of vigilance, the results of this study will be more broadly comparable with other studies.

I excluded any focal sessions where predators or extragroup conspecifics were encountered from analyses as these encounters resulted in increased levels of vigilance and there was no way to ensure that all males were equally sampled under these conditions. I also excluded those focal sessions during which a male was separated from his social group as these animals displayed heightened vigilance levels, particularly while calling and trying to locate their group. In order to keep group composition consistent, I also excluded those samples that were taken on focal subjects within the group when one or more coresident males were absent. Following Rose and Fedigan (1995) and Gould *et al.*(1997), I have expressed social and non-social vigilance as the percentage of time each focal male was observed.

Data analysis

Data were compared separately for each of the three emigration events. First, I compared the vigilance behavior (social and non-social) for the two subject males remaining in the Los Valles group between the two rounds of data collected before and the two rounds of data collected after the emigration of their coresident male (approximately 20 hours before and 20 hours after for each male). To account for factors other than the emigration of a coresident male that may influence male vigilance behavior (e.g. seasonal and/or ecological changes), I used the subject males residing in the CP (N=2) and BH (N=3) groups as a control group. The social and non-social vigilance of the BH and CP males was also compared for the two rounds of data collected before and after the emigration of the LV coresident male. I did not use the remaining CU male in the control group as he was in the process of changing groups during the period after the LV male's emigration which may have influenced his vigilance rates. The CP and BH subject males

were used as a control group, because they did not experience any changes in their group compositions during the LV comparison periods. Therefore, any significant changes in male vigilance behaviors between the before and after periods for these two groups, were not the result of an emigration event and may help identify any extraneous influences on vigilance behavior.

I also control comparisons for the BH and CU emigration events. The control group for the comparison periods before and after the emigration of the BH coresident male consisted of the six males residing in the three remaining study groups (LV N=3, CP N=2; and CU N=1). The control group for the CU male's emigration consisted of 9 males residing in the three remaining study groups (LV N=3; CP N=2; BH N=4).

I used a two-tailed Wilcoxon paired sample test (Zar, 1999), to compare the social and non-social vigilance of the control groups before and after the emigration of their test group's coresident male. I then described the changes in the vigilance of test groups with their control groups. Test group sample sizes are too small to allow for further statistical comparisons.

RESULTS

Los Valles emigration:

Table 4.2 summarizes the changes in vigilance behavior for the control group and the two remaining Los Valles (LV) males before and after the emigration of their coresident male. The non-social vigilance of both LV males decreased after the emigration of their coresident male (mean before =1.37%; mean after =0.81%). The change in non-social vigilance for the control group was non-significant (Z=-0.135; p=.89), with the mean decreasing from 0.73% to 0.72% after the LV emigration event. Both LV males also displayed a decrease in their social vigilance after their coresident's disappearance, with the mean percentage of time these males engaged in social vigilance falling from 10.59% to 7.75%. All of the control males (N=5) displayed an increase in their social vigilance during the comparison period and the group's mean percentage

of time engaged in social vigilance increased significantly from 4.64% to 7.79% (Z=-2.023; p=.043).

Bosque Humedo emigration:

The non-social vigilance of the three remaining BH males increased from 0.55% to 1.00% after the emigration of their coresident male (Table 4.3). The control males (N=6) also displayed a slight increase in non-social vigilance during this time, from 0.84% to 0.86%, but this change was non-significant (Z=-0.943; p=.345). The remaining BH males exhibited a decrease in the percentage of time devoted to social vigilance after the emigration of a coresident subadult male, with their mean falling from 5.94% to 3.68%. The control males also displayed an overall decrease in their social vigilance during this time period, however, the decrease from 7.81% to 6.35% was non-significant (Z=-0.943; p=.345).

Cuajiniquil emigration:

The sole remaining male in the CU group decreased the time he devoted to non-social vigilance, from 4.14% to 1.89%, after the emigration of his coresident male (Table 4.4). All of the control males also exhibited a decrease in their non-social vigilance between the comparison periods, with their mean falling from 6.49% to 1.02%, and this decrease was significant (Z=-2.666; p=.008). The CU male displayed an increase in his social vigilance, from 7.37% to 11.38%, after the emigration of his only coresident male. The control males (N=9) displayed an overall decrease in their mean social vigilance during the period after the emigration of the CU male (mean before= 8.45%; mean after=6.79%). This decrease was non-significant (Z=-1.599; p=.11) and three of the nine control males increased their social vigilance during this period.

DISCUSSION

Effect of male emigration on coresident male non-social vigilance

Traditional investigations of predation and vigilance indicate that individual non-social vigilance levels should increase with decreasing group size (e.g. Hamilton, 1971; Bertram, 1980; Yaber and Herrera, 1994) and fewer numbers of males (van Schaik and van Noordwijk, 1989; Rose and Fedigan, 1995). Given these previous findings, I predicted that male non-social vigilance would increase after the emigration of a co-resident male. However, of the three test groups only the Bosque Humedo males behaved as predicted. The mean level of non-social vigilance for the BH test group nearly doubled as it increased from 0.55% to 1.00% after the departure of their coresident male, and although the control group also displayed a slight increase over the comparison period (.84% to .86%), it was non-significant. This indicates that the more substantial increase observed for the BH group was the result of the emigration event rather than general ecological changes occurring during that time.

It is particularly interesting to note the substantial increase in the non-social vigilance of the BH alpha male, Leo. Alpha male white-faced capuchins often search for missing coresident males (Perry 1998a, 1998b), and it is possible that Leo's increased vigilance behavior was aimed at locating his missing coresident. However, the "after emigration" period of comparison commenced 20 days post emigration, and with no lost calling or searching noted during data collection, this is an unlikely explanation for Leo's heightened vigilance. It is also important to consider the fact that Leo was the only adult male in the BH study group. His two remaining coresident males were subadults; they contributed relatively little in the way of non-social vigilance, and their mean proportion of time spent in non-social vigilance, at .42%, is well below that of Leo and the mean for the control males.

For the two remaining emigration events, LV and CU, the test groups responded counter to my prediction. After the LV male's disappearance, his coresident males decreased rather than increased their non-social vigilance efforts. Similarly, the CU alpha male also displayed a

decrease in his non-social vigilance behavior after the emigration of his only coresident male. Non-social vigilance represents an individual's perception of risk, predation or otherwise, so why then would these males have exhibited a decrease in their non-social vigilance after the emigration of a coresident male?

The substantial decrease in non-social vigilance of the CU alpha male, Spike, is best explained by seasonal changes. Due to the timing of the CU coresident male's (Garth) emigration (May 1998), data for this group were compared between the dry and wet seasons. My finding that the control group displayed a significant decrease in their non-social vigilance at this time indicates that the change in season had an overall effect on male vigilance levels. A decrease in male vigilance during the wet season is expected as white-faced capuchins in Santa Rosa cease using terrestrial waterholes. Burger and Gochfeld (1992) note that waterholes are areas of high predation risk, and Rose and Fedigan (1995) found that male vigilance increased at terrestrial waterholes. Rose (1988) notes that low levels of rainfall can lead not only to decreased food availability, but to increased vertebrate predation, decreased tree coverage, and increased use of terrestrial waterholes, all of which influences male non-social vigilance behavior.

Despite these seasonal effects on male non-social vigilance, Spike's level after the emigration of his only coresident male was still higher at 1.89% than the mean for the control group (1.02%). This increased time Spike devoted to non-social vigilance in comparison to the control group was also not attributable to his searching and lost calling for his missing coresident (Perry, 1998a, 1998b) as the " after emigration" period occurred almost 5 weeks following the last observation of Garth within the CU group. It is possible however, that Spike was still monitoring the location of Garth, who emigrated to the neighboring Cafetal group with a range that substantially overlapped with that of the CU group. This explanation is strengthened by the fact that Spike entered the Cafetal group on several occasions and eventually took over as the group's alpha male. Another possible explanation for Spike's high level of non-social vigilance in comparison with the control group is that after Garth's emigration, the CU group became a uni-male group,

the only one in this study. Spike's above average non-social vigilance may indicate that coresident males are taking up some of the burden of watching for predators and extragroup conspecifics, as was predicted in this study.

The decrease in the LV males' non-social vigilance is more problematic. The control group did not significantly alter their non-social vigilance over the comparison period, making a seasonal effect an unlikely explanation for the change observed among the test males. The LV males displayed a higher mean rate of non-social vigilance (1.37%) than the control group (0.73%) prior to the emigration of their coresident male (Pirate); after his disappearance from the group, the LV males decreased their non-social vigilance to a level more comparable to that of the control group (LV mean=0.81%; control group mean=0.72%). Prior to his disappearance, Pirate spent much of his time on the periphery of the group. The heightened vigilance of his coresident males during the before comparison period, may have been an attempt to monitor Pirate's movement and keep him in, or out, of the group. This explanation is nonetheless counter to the prediction and indicates that some coresident males may be imposing a cost in terms of the amount of time males must devote to non-social vigilance.

Effect of male emigration on coresident male social vigilance

According to the social monitoring hypothesis, those species with strict dominance hierarchies should devote an increasing amount of time to social vigilance with an increasing number of competitors within the group (Caine & Marra, 1988). Following this hypothesis, I predicted that male social vigilance would decrease after the emigration of a coresident male because the number of competitors within the group had declined. Two of the three test groups, LV and BH, responded according to this prediction. Only the CU male, Spike, displayed an increase in time devoted to social vigilance after the departure of his sole coresident male. Spike's social vigilance increased considerably from 7.37% to 11.38%, in contrast with the mean

decrease displayed by the control group over the comparison periods (mean before=8.45%, mean after=6.79%).

As mentioned above, the vigilance behaviors of the CU male were compared between the dry and wet seasons, and seasonality did have a significant effect on male non-social vigilance. Given that the control group did not exhibit a significant change in social vigilance and that their mean rate actually decreased over the comparison periods, the increase in Spike's social vigilance is not likely the exclusive result of seasonal influences. Spike's increased social vigilance may be better explained by the alteration in behavior that he underwent after the emigration of his only coresident male, Garth. Prior to Garth's emigration, Spike spent 26.4% of his time in contact with group members and 8.02% in proximity (≤ 1meter) to them, for a total of 34.26%. Of this 34.26%, approximately two thirds (22.5%) was spent with Garth. After Garth's emigration from the group, Spike spent only .64% of his time in contact and .77% in proximity with his fellow group members (total = 1.41%). Following Garth's departure, Spike spent the vast majority of his time alone on the periphery and often became separated from the rest of his group. Spike's increased social vigilance may, then, reflect an attempt to monitor the locations of his fellow group members (females and immatures) and decrease the probability that he would become separated from them. It is unclear why Spike withdrew from the rest of his group, but it is interesting to note that he "visited" Garth in his new group on several occasions and eventually joined the group as alpha male in Feb. 1999 with Garth as his beta male. Although it is possible that seasonality may have influenced Spike's social behavior in some way (i.e. his withdrawal from the group), such seasonal changes in sociality were not observed in the other study groups.

As predicted by the social monitoring hypothesis, the remaining two test groups, LV and BH, decreased their levels of social vigilance after the emigration of a coresident male. The LV males decreased their mean proportion of time spent in social vigilance from 10.59% to 7.75%. This effect is strengthened by the finding that the control group displayed a significant increase in the proportion of time they devoted to social vigilance, from 4.64% to 7.79%, over this same period

of time. The similarity in the social vigilance levels of the LV males and the control group after the emigration event further illustrates the effect that the extra coresident male had on their social vigilance. After Pirate's emigration, the composition of LV group more closely approximated the two control groups in terms of the number of coresident males. The LV group contained two adult males in the after period of comparison, as did the CP group; the BH group had one adult and two subadult males.

The BH males also decreased their social vigilance after the emigration of a subadult coresident male (mean before=5.94%, mean after=3.68%), although the group's levels for both the before and after periods were substantially lower than those of the control group (mean before=7.81%, mean after=6.35%). These lower levels of social vigilance during both the before and after periods of comparison may again have been the product of the coresident males being subadults. The smaller size of subadult males, the limited support they receive from group females, and their generally lower competitive abilities, all indicate that they are less of a threat to adult coresident males. This may explain the lower levels of social vigilance observed within this group.

However the BH group's alpha male, Leo, displayed a substantial decrease in his social vigilance after emigration of his subadult coresident male George (mean before=8.72%, mean after=4.58%). George was 9 years old prior to his emigration, making him the oldest of the subadult males, and approaching adulthood. Prior to his emigration, George began displaying heightened levels of aggression. He engaged in frequent chases, lunges and general threats to all group members, with the exception of the alpha male. It is possible that the heightened social vigilance of the BH alpha male prior to George's emigration was the result of this increased aggression and that Leo was perceiving George as a threat to his dominance within the group. George was becoming a competitor increasingly equal in size and strength to the alpha male.

Are male white-faced capuchins benefiting from the presence coresident males?

Mitani *et al.* (1996) suggest that for those species whose multimale structure cannot be explained by female breeding synchrony and female group size, males must benefit from the presence of coresident males in some other way. I addressed this suggestion by testing whether or not coresident males are providing a "service" to one another in terms of reducing the amount of time coresident males devote to non-social vigilance. This "service" would lead to increased protection from both predators and conspecifics in exchange for membership within a social group. I predicted that if males are benefiting from the presence of coresident males in this way, they should increase their time devoted to non-social vigilance after the emigration of a coresident male. Although this prediction was not uniformly supported in this study, the results from the BH group, and perhaps the CU group, indicate that some coresident males are providing a positive service with their non-social vigilance behavior.

The data presented on the effects of male emigration on the social vigilance of coresident males were somewhat more conclusive. Two of the study groups displayed a clear decrease in social vigilance after the departure of a coresident male. The increase in social vigilance displayed by the one male remaining in the third study group (CU) was attributable to the change in behavior that he underwent after the departure of his only coresident male. The presence of multiple coresident males, therefore, does appear to have a cost: males need to spend more time engaged in social vigilance with an increasing number of co-resident males. It also appears that social vigilance levels are affected by the threat that coresident males pose to one another, and that subadult males are less threatening than adult males.

However, the results of this study clearly illustrate the variability in male vigilance behavior in white-faced capuchins and the numerous factors that can influence it. Over the three emigrations (a period of 15 months), the range of time that individual males engaged in both social and non-social vigilance was quite dramatic. Male vigilance behavior may be influenced by seasonality (CU), the cohesion of the group (LV and CU), and even the age of coresident males

(BH). This variability in the data makes it difficult, and unwarranted, to draw any broad generalizations. This said, it does appear that some males are more costly to have as coresidents than others. For example, subadult males contribute less to non-social vigilance than adult males, and they still require social monitoring as evidenced by the BH adult male's high levels of social vigilance in all of the comparisons made (i.e. control and test periods for all three emigrations). The results from the LV group indicate that more peripheral males, those who do not fully integrate themselves within the group, may be particularly costly to tolerate. The two males remaining in the LV group decreased the amount of time they engaged in both social and non-social vigilance, indicating that they were investing a larger percentage of their time monitoring the location and behavior of their peripheral coresident male.

Regardless of the costs that males are imposing on one another, the very presence of multiple coresident males appears to provide an important benefit to both females and males. Male takeovers in white-faced capuchins have resulted in the eviction of resident males, infanticide, and the deaths or disappearances of both males and females (e.g. Rose and Fedigan, 1995). An increased number of males residing within a heterosexual group appears to reduce the chance, or at least the success, of male takeovers (Perry 1998a, 1998b). From this cumulative evidence, Rose and Fedigan (1995) suggest that females may benefit from a reduction in the possible harm they and their kin might incur if they live in groups with multiple males. This may also be the main benefit to males. Long-term data from Santa Rosa demonstrates that once an alpha male loses the support of subordinates due to emigration, he is no longer able to defend the group from the immigration attempts of extra-group males. It may not be that males necessarily want to reside in groups with multiple males but, rather, that they need to. Male white-faced capuchins have great difficulty not only joining, but also remaining in, a social group without the support and cooperation of other males.

Table 4.1 Composition of study groups for comparison period and date of coresident male emigration.

Group	Adult Males	Subadult Males	Adult Females	Immatures	Total	Date of coresident male emigration
CP	2	0	3	3 – 5	8 – 10	No emigration; group included in analyses as a control group
LV	2 – 3	0	4	6 - 8	12 - 15	Dec. 1998
BH	1	2 – 3	3	1	7 - 8	Nov. 1998
CU	1 – 2	0	1	3	5 - 6	May 1998

Table 4.2 Male social and non-social vigilance before and after the emigration of the Los Valles coresident male (expressed as % of time spent in each activity).

Group	Social Before	Social After	Non-social Before	Non-social After
Test Group:				
Diablo (LV;ad;)	9.53	7.79	1.37	1.15
Side (LV;ad)	11.64	7.70	1.36	0.46
Mean	10.59	7.75	1.37	0.81
Control Group:				
Nose (CP;ad;)	7.46	11.53	0.61	1.65
Trickle (CP;ad)	4.07	5.91	0.22	0.66
Leo (BH;ad;)	5.01	10.17	1.98	0.81
Regis (BH;sa)	3.06	6.03	0.37	0.24
Casey (BH;sa)	3.58	5.30	0.42	0.27
Mean	4.64	7.79	0.73	0.72
Wilcoxon paired sample test (2 tailed)	Z=-2.023[a]	p=.043*	Z=-0.135[b]	p=.893

LV = Los Valles; BH= Bosque Humedo; CP = Cerco de Piedra
ad = adult male; sa = subadult male; = Alpha Male
a. based on positive ranks
b. based on negative ranks
*significance set at <.05

Table 4.3 Male social and non-social vigilance before and after the emigration of the Bosque Humedo coresident male (expressed as % of time spent in each activity).

Group	Social Before	Social After	Non-social Before	Non-social After
Test Group:				
Leo (BH;ad;)	8.72	4.58	0.92	2.17
Regis (BH;sa)	5.31	3.10	0.39	0.42
Casey (BH;sa)	3.79	3.37	0.35	0.42
Mean	5.94	3.68	0.55	1.00
Control Group:				
Diablo(LV;ad;)	6.97	8.11	1.28	1.26
Side (LV;ad)	11.60	11.61	1.13	1.38
Pirate (LV;ad)	8.41	4.93	0.56	1.02
Nose (CP;ad;)	6.10	6.98	0.57	0.76
Trickle (CP;ad)	4.79	3.38	0.22	0.30
Spike (CP;ad;)	9.00	3.09	1.26	0.41
Mean	7.81	6.35	0.84	0.86
Wilcoxon paired sample test (2 tailed)	Z=-0.943[a]	p=.345	Z=-0.943[a]	p=.345

LV = Los Valles; BH = Bosque Humedo; CP= Cerco de Piedra; CU = Cuajiniquil
ad = adult male; sa = subadult male; = Alpha Male
a. based on positive ranks

Table 4.4 Male social and non-social vigilance before and after the emigration of the Cuajiniquil coresident male (expressed as % of time spent in each activity).

Group	Social Before	Social After	Non-social Before	Non-social After
Test Group:				
Spike (CU;ad;)	7.37	11.38	4.14	1.89
Control Groups:				
Diablo (LVad;)				
Side (LV;ad)	10.18	6.68	5.79	0.36
Pirate (LV;ad)	11.62	8.44	5.97	1.88
	7.86	8.80	7.88	1.01
Nose (CP;ad;)				
Trickle (CP;ad)	6.00	7.88	12.80	1.68
	4.10	5.26	6.70	1.05
Leo (BH;ad;)				
Regis (BH;sa)	8.52	9.14	8.28	1.14
Casey (BH;sa)	7.70	5.90	1.17	0.68
George (BH;sa)	6.60	4.26	4.68	0.93
	13.45	4.72	5.15	0.44
Mean	8.45	6.79	6.49	1.02
Wilcoxon paired sample test (2 tailed)	Z=-1.599[a]	p=.110	Z=-2.666[a]	p=.008*

LV = Los Valles; BH = Bosque Humedo; CP= Cerco de Piedra; CU = Cuajiniquil
ad = adult male; sa = subadult male; = Alpha Male
a. based on positive ranks
*significance set at <.05

REFERENCES

Altmann, J. 1974. Observational study of behavior: Sampling methods. *Behav.*, 49: 227-266.

Altmann, J. 1990. Primate males go where the females are. *Anim. Behav.*, 39: 193-195.

Baldellou: M., and Henzi: S.P. 1992. Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Anim. Behav.*, 43: 451-461.

Bertram, B.C.R. 1980. Vigilance and group size in ostriches. *Anim. Behav.*, 28: 278-286.

Blumstein, D.T. 1996. How much does group size influence golden marmot vigilance? *Behav.*, 133: 1133-1151.

Burger, J., and Gochfeld, M. 1992. Effect of group size on vigilance while drinking in the coati, *Nasua narica*, in Costa Rica. *Anim. Behav.*, 44: 1053-1057.

Caine, N.G., and Marra: S.L. 1988. Vigilance and social organization in two species of primates. *Anim. Behav.*, 36: 897-904.

Chapman, C.A. 1986. Boa constrictor predation and group response in white-faced Cebus monkeys. *Biotropica*, 18: 171-172.

Cowlishaw, G. 1998. The role of vigilance in the survival and reproductive strategies of desert baboons. *Behav.*, 135: 431-452.

Dunbar, R.I.M. 1988. *Primate Social Systems*. Comstock Publishing Associates, New York.

Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, 197:215-223.

Fedigan, L.M. 1993. Sex differences and intersexual relations in adult white-faced capuchins *Cebus capucinus*. *Int. J. Primatol.*, 14: 853-877.

Fedigan, L.M., Rose, L.M., and Avila, R.M. 1997. See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In *Adaptive Radiations of Neotropical Primates,* (M. Norconk, A. Rosenberger and P. Grabber eds.). Plenum Press, New York & London.

Fragaszy, D.M. 1990. Age and sex differences in the organization of behavior in wedge-capped capuchins *Cebus olivaceus*. *Behav. Ecol.*, 1: 81-94.

Freese, C.H. 1978. The behavior of white-faced capuchins *Cebus capucinus* at a dry-season waterhole. *Primates*, 19: 275-286.

Freese, C.H. 1983. Cebus capucinus Mono cara blanca, white-faced capuchin. In *Costa Rica Natural History* (D.H. Janzen, ed.). University of Chicago Press, Chicago, pp. 458-460

Glander , E.G. , Fedigan, L.M., Fedigan, L., and Chapman, C. 1991. Field methods for capture and measurement of three monkey species in Costa Rica. *Folia Primatol.*, 57: 70-82.

Gould, L., Fedigan, L.M., and Rose, L.M. 1997. Why be vigilant? The case of the alpha male. *Int.l J. Primatol.*, 183:401-414.

Hamilton, W.D. 1971. Geometry for the selfish herd. *J. of Theor. Biol.*, 31: 295-311.

Kappeler, P.M. ed. 2000. *Primate males: causes and consequences of variation in group composition*. Cambridge University Press, Cambridge.

Kerverne, E.B., Leonard, R.A., Scruton, D.M., and Young, S.K. 1978. Visual monitoring in social groups of talapoin monkeys *Miopthecus talapoin*. *Anim. Behav.*, 26: 933-944.

Mitani, J.C., Gros-Louis, J., and Manson, J.H. 1996. Number of males in primate groups: comparative tests of competing hypotheses. *Amer. J. Primatol.*, 38: 315-332.

Nunn, C.L. 1999. The number of males in primate social groups: a comparative test of the socioecological model. *Behav. Ecol. Sociobiol.*, 46: 1-13.

O'Brien, T.C. 1991. Female-male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. *Anim. Behav.*, 41: 555-567.

Oppenheimer, J.R. 1968. *Behavior and Ecology of the White-faced Monkey, Cebus capucinus on Barro Colorado Island, Canal Zone*. Ph.D. dissertation, University of Illinois, Urbana.

Pereira, M.E. 1998. One male, two males, three males, more. *Evol. Anthrop.*, 7: 39-45.

Perry, S.E. 1995. Social relationships in wild white-faced capuchin monkeys *Cebus capucinus*. Ph.D. dissertation, University of Michigan.

Perry, S.E. 1996. Intergroup encounters in wild white-faced capuchin monkeys. *Cebus capucinus*. *Primates*, 35: 409-415.

Perry, S.E. 1998a. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behav.*, 135: 139-172.

Perry, S.E. 1998b. A case report of a male rank reversal in wild white-faced capuchins *Cebus capucinus*. *Primates*, 39: 477-510.

Ridley, M. 1986. The number of males in a primate troop. *Anim. Behav.*, 34: 1848-1858.

Robinson, J.G. 1988a. Demography and group structure in wedge-capped capuchin monkeys, *Cebus olivaceus*. *Behavl.*, 104: 202-232.

Robinson, J.G. 1988b. Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. *Behav. Ecol. Sociobiol.*, 23: 187-197.

Rose, L.M. 1994. Benefits and costs of resident males to females in white-faced capuchins *Cebus capucinus*. *Amer. J. Primatol.*, 32: 235-248.

Rose, L.M. 1998. Behavioral ecology of white-faced capuchins Cebus capucinus in Costa Rica. Ph.D. dissertation, University of St. Louis.

Rose, L.M., and Fedigan, L.M. 1995. Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Anim. Behav.*, 49: 63-70.

Rowe, N. 1996. *The Pictorial Guide to the Primates*. New York: Pogonias Press.

van Schaik, C.P. 1983. Why are diurnal primates living in groups? *Behav.*, 87: 120-144.

van Schaik, C.P. 1996. Social evolution in primates: The role of ecological factors and male behaviour. *Proc. Br. Acad.*, 88: 9-31.

van Schaik, C.P., and van Hooff, J.A.R.A.M. 1983. On the ultimate causes of primate social systems. *Behav.*, 85: 91-117.

van Schaik, C.P., and Höstermann, M. 1994. Predation risk and the number of adult males in a primate group: a comparative test. *Behav. Ecol. Sociobiol.*, 3: 261-272.

van Schaik, C.P., and van Noordwijk, M.A.. 1989. The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behav. Ecol. Sociobiol.*, 24: 265-276.

Smuts, BB., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., and Struhsaker, T.T. (eds.) 1987. *Primate Societies*. Chicago University Press, Chicago.

Steenbeek, R., Ruben, C.P., van Buul, M., and van Hooff, J.A.R.A.M. 1999. Vigilance in wild Thomas's langurs *Presbytis thomasi*: the importance of infanticide risk. *Behav. Ecol. Sociobiol.*, 45: 137-150.

Terborgh, J.W. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton University Press, New Jersey.

Treves, A., and Chapman, C.A. 1996. Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. *Behav. Ecol. Sociobiol.*, 39: 43-53.

Treves, A. 1997. Vigilance and the use of micro-habitat in solitary rainforest mammals. *Mammalia*, 61: 511-525.

Treves, A. 1998. The influence of group size and neighbors on vigilance in two species of arboreal monkeys. *Behav.*, 135: 453-481.

Treves, A. 1999. Has predation shaped the social systems of arboreal primates? *Int. J. Primatol.*, 20: 35-67.

Wrangham, R. 1980. An ecological model of female-bonded primate groups. *Behav.*, 75: 262-299.

Yaber, M.C., and Herrera, E.A. 1994. Vigilance, group size and social status in capybaras. *Anim. Behav.*, 48: 1301-1307.

Zar, J.H. 1999. *Biostatistical Analysis*. Fourth Ed. New York: Prentice-Hall Inc.

CHAPTER FIVE

Affiliative relationships among male white-faced capuchins (*Cebus capucinus*): Evidence of male-bonding in a female bonded species.

INTRODUCTION

Early studies of relationships among male primates focused on the aggressive nature of intramale competition within groups (van Hooff, 2000). These initial studies led to the assumption that constant male intrasexual competition gave rise either to the complete exclusion of male competitors in the form of uni-male groups, or the formation of rigid dominance hierarchies in which dominant males have priority of access to mates (ibid.). However, as long-term studies on non-human primates increase, we are beginning to realize that relationships among males are not that straightforward and that males may well display greater levels of diversity in their relationships than females (van Hooff & van Schaik, 1994).

Many species of non-monogamous primates reside in groups characterized by female philopatry and male dispersal (Pusey & Packer, 1987). Relationships among females in female philopatric groups vary from egalitarian to neutral and reflect the nature of resource competition within and between groups (Sterck *et al.* 1997). Sometimes strong bonds based on the maintenance of close proximity, grooming and coalitionary interactions form between group females in female philopatric species (Wrangham, 1980; van Hooff, 2000). As a result of the male-biased pattern of dispersal, females within these groups are usually closely related to one another and their shared kinship and familiarity are thought to facilitate the formation of close bonds (van Hooff, 2000; van Hooff & van Schaik, 1994). Such species have been traditionally referred to as female-bonded (Wrangham, 1980) and more recently as resident nepotistic (Sterck *et al.*, 1997).

Relationships among coresident adult males also vary greatly within groups and across primate species. They range from despotic to affiliative and cooperative, and these relationships appear to be somewhat dependent upon the dispersal pattern of a particular species (see Silk,

1994 for review). The majority of species for which strong bonds among coresident males have been reported are male philopatric (e.g. red colobus: Strusaker & Leland, 1987; spider monkeys: Fedigan & Baxter, 1984; chimpanzees: Goodall 1965, 1986; Costa Rican squirrel monkeys: Boinski, 1994; but see Strier, 1994 on male muriquis). This correlation between male-bonding and male philopatry led to an initial assumption that kinship was a necessary precursor for bonding to occur (van Hooff, 2000; van Hooff & van Schaik, 1994). However, there is increasing evidence for a number of species that collaborative and affiliative bonding may occur in the absence of kinship (for reviews see Pereira *et al.*, 2000 and van Hooff, 2000; bonnet macaques: Silk, 1994; macaque sps.: Hill, 1994). Recent studies of male-bonding in chimpanzees, the classic example of a male-bonded species, have also found that bonds are frequently formed among males who are nonmaternal kin (Goldberg & Wrangham, 1997; Mitani *et al.*, 2000).

Despite the increasing evidence of male-bonding in the absence of kinship, many species of female philopatric primates are characterized by stronger affiliative bonds among females rather than males. Van Hooff and van Schaik (1994) suggest that affiliative bonds are less likely to occur among males than among females, simply as a result of the fundamentally different strategies the sexes employ to maximize inclusive fitness. A female's fitness is dependent upon her ability to survive and continue reproducing, which in turn is dependent upon her access to resources. Competition between females, therefore, usually occurs in the context of resource acquisition (Wrangham, 1980). The inclusive fitness of a male, on the other hand, is dependent primarily on the number of females he can successfully inseminate. Males, therefore, compete mainly for access to females. Van Hooff and van Schaik (1992) suggest that because fertilizations cannot be shared in the same manner as food and other resources, the likelihood of cooperative and affiliative relations among males is limited.

This competition between males for access to fertilizations may explain why, for the majority of multimale species characterized by male dispersal and female philopatry, male relations are primarily competitive or neutral (van Hooff, 2000). However, in species where dominant males

benefit from the presence of subordinate males, some sort of "staying incentive", usually in the form of shared reproduction, is expected. Van Hooff (2000) suggests that multimale groups arise for one of two reasons: dominants are unable to keep rivals out, or coresident males are tolerated because they provide some benefits. Perry (1996b, 1998a) and Rose and Fedigan (1995) have demonstrated that both of these conditions apply to white-faced capuchins; subordinate males are tolerated because their cooperation in excluding extragroup males is essential if the alpha male is to retain residency within a group.

White-faced capuchins reside in multimale-multifemale groups in which females are generally philopatric and males disperse (Fedigan, 1993; Oppenheimer, 1968). Females within groups maintain long-term affiliative relationships with one another, evidenced by stable partner preferences for grooming, proximity, and coalitionary support, and the species is generally considered to be female-bonded (Fragaszy *et al.*, in prep.; Perry, 1996a). Males are the transient group members, making durational bonds between them more difficult. However, we have increasing evidence that some males do form close affiliative bonds with one another and that these bonds last over several migrations (Chapter 3).

Changeovers in male membership within groups of white-faced capuchins occur approximately every 3-4 years in the form of male takeovers (Fedigan, 1993; Fedigan *et al.*, 1996; Rose, 1998, 1994a; Rose & Fedigan, 1995; Perry, 1998a, 1998b). These takeovers involve several extragroup males (2-4) approaching a heterosexual group and eventually supplanting the resident males. During these takeovers, the interactions among males are described as being violent, and males are reported to suffer the most serious wounding during immigration attempts. Male takeovers at Santa Rosa have resulted in the eviction of resident males, infanticide, and the deaths or disappearances of both males and females. It is suspected that an increased number of males residing within a heterosexual group reduce the chances, or at least the success, of male takeovers (Perry, 1998a, 1998b; Rose & Fedigan, 1995).

Despite the cooperation of male white-faced capuchins in defending the group against extragroup males, van Hooff (2000) points out that such cooperation is not necessarily associated with high levels of male affiliation. This appears to be the case for white-faced capuchins where male-male relationships across groups are extremely variable, regardless of the cooperative nature of group males during encounters with extragroup individuals. For example, Perry (1998b) described male-male relationships in her study group at Lomas Barbudal, Costa Rica, as being tension-loaded and more aggressive than affiliative, and Oppenheimer (1968), Mitchell (1989) and Rose (1994b) all reported that males exchange few affiliative interactions with one another. In contrast with these findings, Fedigan (1993) found that males in her Santa Rosa study groups groomed and affiliated with one another more frequently than they did with group females and Perry (pers. comm.) also reports higher levels of male affiliative interactions in her new study group at Lomas Barbudal.

Why are relationships among male white-faced capuchins so variable, and what factors affect the quality of male relationships? In this study I examine the social relationships of all adult (N=8) and subadult male (N=3) white-faced capuchins residing in four social groups in Santa Rosa National Park, Costa Rica. The goals of this paper are to (1) compare male-male and male-female affiliative relationships to determine with which sex males are more closely bonded; and (2) quantitatively examine male dyadic relationships within the study groups to determine why some males are more closely bonded than others and what factors influence these relationships.

METHODS

Study site, species and subjects

Data for this study were collected in the Santa Rosa Sector of the Area de Conservacion Guanacaste, Costa Rica. Santa Rosa encompasses approximately 10, 800 ha. of dry deciduous forest and reclaimed pasture and is located 35 kilometers northwest of Liberia, in the Guanacaste

Province. Observational and demographic data have been collected on the white-faced capuchins in Santa Rosa by Dr. Linda Fedigan, University of Alberta, and her students since 1983.

White-faced capuchins reside in multimale-multifemale social groups comprised of related females, their offspring, and immigrant males (Oppenheimer, 1968; Freese, 1978; Fedigan, 1993). This is a sexually dimorphic species with males being an average of 25-35% larger than females and individually dominant to them, with the exception of the alpha female (Fedigan, 1993). In Santa Rosa the mean capuchin group size is 17.2 with sex ratios approximating 1:1 (Fedigan & Jack, in press 2001). White-faced capuchins are not seasonal breeders, but they do display a birth peak between January and April (Fedigan *et al.*, 1996).

From February 1998 through April 1999 my assistants and I observed 8 adult (>10 years) and 3 subadult (7-10 years) males residing in four distinct social groups in Santa Rosa: Cerco de Piedra (CP); Los Valles (LV); Bosque Humedo (BH); and Cuajiniquil (CU) (see Appendix A for relative locations of group home ranges). All of the males in these groups were habituated to the presence of observers and, with the exception of two more recently immigrated males, they had been previously included in behavioural studies. Several of these males have been observed since their birth. All members of the four study groups (males, females, and immatures) were habituated to the presence of researchers and observations could easily be made from 5 – 10m. Members of the study groups were individually recognized and identified according to their size, facial characteristics, and brow shape.

A fifth study group, the Cafetal group (CA), was also observed during February and March 1999. The two males from the Cuajiniquil group had transferred to the neighboring Cafetal group; the first immigrated between June and August 1998 and the second followed in February 1999. Behavioral data were only collected on these two males during this period. All other members of the Cafetal group were individually known and habituated by the observers prior to the commencement of data collection (see Appendix A for the location of the Cafetal group in relation to the four main study groups).

Data collection

A total of 1198.25 hours of focal data were collected on the 11 subject males. Data were collected in 15-minute focal animal continuous-time samples (Altmann, 1974) during which all behaviours and interactions were recorded directly into a handheld PSION computer using the FOCOBS data entry program designed by Dr. Joan Silk at the University of California, Los Angeles. Efforts were made to sample all focal males for 10 hours before moving on to the next study group. A focal session was discarded if the subject was out of sight for ≥ 120 sec. during the 15 min session. To ensure inter-observer reliability my assistants and I spent several weeks practicing data collection together in the field prior to the commencement of the study.

Dependent variables (affiliative behaviours)

Four measures of affiliative relationships were examined: total contact; contact rest; grooming; and proximity. Total contact includes any behaviour during which a subject male engaged in non-aggressive body contact with another group member. This includes resting in contact, grooming (received and directed), playing, scanning, and foraging while in contact. Contact rest and grooming rates (directed and received) are subsets of total contact. Proximity was recorded continuously throughout a focal session when a male was within one meter of another group member, excluding body contact. All of these behaviors were recorded as states and the duration of each was calculated in average seconds per hour following Perry (1998a, 1998b). Durations of male-male dyadic affiliation were calculated as the average number of seconds per hour that the two males affiliated. That is, the total time each partner interacted with one another was combined and then divided by the combined hours each partner was observed.

Independent variables

Five variables were investigated as possible factors influencing male-male relationships within groups: age relationship between males; group size; sex ratio (M:F); rank distance; and

duration of relationship between males. For the first variable, age-relationship between males, the 11 dyads were divided into the following categories: adult-adult, adult-subadult, and subadult-subadult. Group size and sex ratio were also examined as variables influencing male relationships within groups. Data were collected over 15 months during which time three of the study groups experienced changes in group composition. To keep group size and sex ratio constant it was necessary to use a subset of the focal data collected on several of the subject males. For example, one of the Bosque Humedo (BH) subadult males, George, emigrated six months into the study causing a change in both group size and sex ratio. For the remaining three BH males I have included data that were collected after George's emigration (with the exception of the dyadic interactions that included George). This is why the sex ratio for this group varies in Table 5.1. To simplify interpretation of the results presented, I have included the number of hours of focal data utilized to calculate the affiliative behaviours in each set of analyses (see column 1 in Tables 5.2 and 5.3).

The rank of each adult and subadult male within study groups was calculated according to the direction of submissive gestures and avoid-supplant interactions observed during focal and *ad libitum* data collection. Rank distance was calculated following Rose (1998), whereby the rank of the dominant individual was subtracted from that of the subordinate dyad partner. For example, the rank distance for a dyad containing the 3rd ranked male and the alpha male is 2. The final variable investigated was the duration of the relationship between dyad partners. Life history data were available for many of the males in the study groups, with only two previously unknown males having entered into the study groups over the last 2 years. The duration of the relationship between males was calculated as the minimum number of months the males have resided with one another in one or more groups. This information was made available by Dr. Linda Fedigan. The values of the five independent variables for each of the focal males are presented in Table 5.1.

Data analysis

Two-tailed Wilcoxon signed ranks tests were used to compare the time males spent affiliating with females versus coresident males. Multiple regression analyses were then used to examine the predictive value of the five independent variables (age relationship, group size, sex ratio, rank distance, and relationship duration) on each measure of affiliation for male-male dyads (total contact, contact rest, groom, and proximity). All dependent variables were logarithmically transformed to fit a linear model (Zar, 1999) and only those variables that resulted in significant simple linear regressions were entered into the final models. Significance was set at 0.012 to compensate for the number of tests run on the data.

RESULTS

Comparison of inter and intrasexual interactions

Males spent an average of 353.52 sec/hr, or 9.8% of their time, in contact with at least one other group member (males, females, immatures) (Table 5.2). With the exception of time spent grooming, males spent a higher mean time affiliating (contact, contact rest, proximity) with group males than females, although none of these differences were significant (the results are summarized in Table 5.2).

Male-male dyadic interactions

Male dyads spent an average of 89.49 sec/hr in non-aggressive contact, with dyadic contact time varying between 3.95 sec/hr to 483.44 sec/hr (Table 5.3). Of the variables investigated, group size and the duration of the relationship between males were the only variables that had a significant effect on the amount of time males spent in contact. Together these variables explained 76% of the observed variation in male dyadic contact time (r^2=.76, F=12.79, p=.003). These data indicate that males residing in smaller groups spend more time in contact with their

coresident males, and the longer males have known each other (i.e. resided in groups together) the more time they spend in non-aggressive contact.

Grooming frequencies for male dyads varied between 0.32 sec/hr to 31.41 sec/hr with a mean of 10.03 sec/hr (Table 5.3). The regression model for male dyadic grooming interactions included group size, sex ratio, relationship duration, and age relationship. For this final variable, age relationship, dyads containing two subadult males differed significantly from those with two adults, and adult and subadult combinations. Together these four variables accounted for 90% of the variation observed in male-male grooming behavior (r^2=.90, F=12.96, p=.004). According to these data, it appears that coresident males residing in smaller groups groom one another more than males residing in larger groups; males in groups with more equivalent sex ratios will groom one another more frequently than males residing in groups with more disparate sex ratios; the longer coresident males have resided together the more they exchange grooming interactions; and, dyads including two subadult males will groom one another more than dyads containing either two adult males, or an adult and subadult male.

Male dyads rested in contact for a mean of 65.00 sec/hr, ranging from 1.48 sec/hr to 453 sec/hr (Table 5.3). Group size was the only variable investigated that had a significant effect on the amount of time males spent resting in contact with one another and it alone explained 60% of the observed variation (r^2=.60, F=13.7, p=.005). Similar results were obtained for the amount of time male dyad partners spent in proximity to one another; only group size had a significant effect on the duration of dyadic proximity, although slightly less of the variation, 53%, is explained by this model (r^2=.53, F=9.928, p=.012). The amount of time male dyad partners spent in proximity varied from 0.38 sec/hr to 390.99 sec/hr with a mean of 63.74 sec/hr. Both the time male dyads spent resting in contact and in proximity to one another were negatively associated with group size. That is, males residing in larger groups generally spent less time resting in contact with, or in proximity to, coresident males.

DISCUSSION

The results obtained in this study further confirm that the relationships among coresident male white-faced capuchins are highly variable between groups. In some groups males preferentially affiliate with adult females while others spend the majority of their time in the company of coresident males. However, the range of variation in the amount of time males spent affiliating with coresident males was much higher than that between males and females (with the exception of grooming). The relationships among the males in my four study groups ran the gamut; the LV and CP males would be best described as displaying neutral and tolerant relationships while the BH and CU males were highly affiliative. For example, if we look at the amount of time males spent in contact with one another, the LV males spent an average of 15.22 sec/hr, CP males 24.25 sec/ hr, BH males 168.45 sec/hr, and the CU males 483.53 sec/hour. Aggressive interactions were rarely observed among any of the males in the four study groups (Jack, unpublished data) indicating, even in the LV and CP groups where males did not frequently affiliate, that male relationships are best characterized as being tolerant and neutral.

These data, accompanied by previous reports of the diversity in the relationships among male white-faced capuchins not only between study sites (e.g. Fedigan, 1993; Perry, 1998b) but between groups within the same sites (i.e. Santa Rosa groups; Fedigan, 1993; Rose , 1994b), lead one to question what factors influence the quality of male relationships in this species. Why are some males more closely bonded than others? Of the independent variables investigated for their association with male affiliative relationships, group size was the most informative. It was significant in explaining a high percentage of the variation among male dyads for all four measures of affiliation. In all cases group size was negatively associated with the amount of time male dyads engaged in the affiliative behaviors. Therefore, among the males in my four study groups, those residing in the smaller groups were more affiliative towards one another than those residing in the larger groups.

Hill (1994), in his review of available literature on relationships among male macaques (sps.), found that affiliative behaviour is also more frequent in smaller groups, although sex ratio also played an important role in his findings. Of the four affiliative measures investigated, sex ratio was the only significant variable in explaining grooming interactions. In the present study, males residing in groups with sex ratios approaching equality groomed more frequently than males in groups with more disparate sex ratios (lower ratio of males to females). Hill (1994) points out that in groups with highly skewed sex ratios (fewer males to females) there are more potential female and immature partners to affiliate with than in those groups with similar ratios of males to females. In small groups this will also be a factor as there is a shortage of potential partners, and males may alternatively need to form relationships with other males.

This may be the case in my study groups, particularly in the Cuajiniquil group which was comprised of only 6 members (2 adult males, 2 adult females one of which was nulliparous, and two immature females). In fact, all four of the study groups were much smaller than the park-wide mean of 17.2 (Fedigan & Jack, in press). These small group sizes (LV 14; CP 9; BH 8-9; CU 6) may explain the affiliative nature of males in the CU and BH groups and the more neutral relationships among the LV and CP males. However, additional data I collected on the two most affiliative males in my study, Spike and Garth, may shed some insight into Hill's proposition. Spike and Garth were members of the smallest study group (CU) which was comprised of only six group members with a sex ratio of 1. Within this group, affiliative partners were indeed scarce, and this may have been what ultimately led to Garth's emigration from the group in mid May 1998 and subsequent transfer into the neighboring Cafetal group by August 1998. In February 1999, Spike joined Garth and took over as the Cafetal group's alpha male (note: Garth was a subordinate male in Cafetal prior to Spike's arrival). Although the Cafetal group, with its 14 members, was still small in comparison to the park mean, the sex ratio was lower, at 0.80, than that of the Cuajiniquil group and the number of available partners was almost triple.

Although the data were not included in this study, we collected over 50 hours of focal data on Spike and Garth in this new group (over a two month period). These two males remained one another's preferred affiliative partners, although to somewhat lesser extent. While in the Cafetal group, Spike spent 158.44 sec/hr in contact with Garth as opposed to 481.1 sec/hour in the CU group. Garth spent 152.4 sec/hr in contact with Spike while in the Cafetal group in comparison to 486 sec/hour in the Cuajiniquil group. These levels are now more on par with those of the BH group males, but still much higher than the males of the LV group, which had the same number of members and a slightly lower sex ratio (0.75). Fedigan (1993) also reported high levels of male-male affiliation in her two study groups of white-faced capuchins in SRNP, with males spending significantly more time affiliating with coresident males than females. Although one of her study groups was small, containing only 12 animals, the other was much larger at 23 members, making the unavailability of partners an unlikely explanation. Combined with the information presented on the Cafetal group, these data indicate that the relationships among males may not be easily defined by the number of available partners within a group.

Perhaps the most informative of the five independent variables investigated was the duration of the relationship between males. In this study there was a significant positive correlation between the number of months male dyad partners have resided together (often in more than one group) and the amount of time they spent in non-aggressive contact and in grooming interactions. Kinship and familiarity have long been assumed to facilitate the formation of bonds between males and there is increasing evidence of a tendency towards above average relatedness between males in those species characterized by male tolerance or male-bonding (van Hooff, 2000). This may well be the case even for a female philopatric species such as white-faced capuchins. Male relatedness may be retained through parallel emigration, whereby males from the same age cohort may emigrate together or males may immigrate into groups containing older, familiar, males. As the data on the Santa Rosa capuchins accumulates, a picture of male migration patterns is beginning to emerge. We have observed young natal males changing groups together, coresident

adult and subadult males collectively emigrating and taking over neighboring groups, and males immigrating into new groups containing males who disappeared from our study groups as many as five years previous (Chapter 2; Chapter 3). We cannot, of course, be certain of the relatedness between males in the absence of concrete genetic data, and this is currently being investigated in my study groups using microsatellite markers obtained from follicular and fecal DNA. However, if it turns out that these males are not kin, the evidence of long-term maintenance of relationships between males over multiple migrations remains, and we know that some males are forming lasting alliances.

Once again, we can consider the example of Spike and Garth of the Cuajiniquil/Cafetal group. These two males engaged in far higher rates of affiliative interactions with one another than they did with any other group members, and their rates were over double those observed for any of the other group males. As far as we know, Spike and Garth have been together longer than any of our other study animals. Spike has been under observation in Santa Rosa since his birth in 1987 (Fedigan, unpublished data). Although we are unable to pinpoint Garth's exact origins, we do know that he was either born into Spike's natal group in 1988 (possible paternal sibling) or in 1989 (maternal sibling), or he is an unrelated male who was a member of the Los Valles group which Spike joined in 1991 (Fedigan, unpublished data). The males born into Spike's natal group in 1988 and 1989 also immigrated into the LV group in 1991 (with Spike) and 1992 respectively. From this long-term data we do know that these two males had resided in the same group for a minimum of 86 months and perhaps as many as 117, and they are quite possibly maternal or paternal siblings. The long-term relationship between these two males may be a rarity and only further studies of males, through multiple migrations, will clarify this issue.

One of the Los Valles male dyads is a case in point. Diablo and Pirate had resided together at least since 1993 (72 months) but they exchanged little in the way of affiliative interactions. In fact, Diablo and Pirate displayed the lowest dyadic rates of contact rest, groom, and proximity in the study. In 1993, these two males appeared independently in the neighboring CP group, Pirate

as an adult male and Diablo as a subadult (Fedigan, unpublished data). Although we are uncertain if these males were from the same group (i.e. parallel emigration), we do know that they immigrated into the CP group during the same month, Diablo in early January with two other adult males, and Pirate later that same month. In 1997 Diablo and Pirate cooperatively overtook the neighboring Los Valles group, with Diablo emerging as the group's new alpha male. These two males, along with Side who joined as a permanent LV member a few months after the takeover, cooperated with one another in defending the group during intergroup and predator encounters (Jack, unpublished data) but their relationship was never particularly affiliative. The rates at which the three LV males affiliated with one another were considerably lower than the rates for the BH, CU and CP group males and Diablo spent the vast majority of his time in the company of the group's females. Pirate disappeared from the LV group in December 1998, and towards the end of his stay in the group he became much less active during intergroup encounters and often kept to himself on the periphery of the group.

These observations indicate that although the length of time males have resided together may be an important factor influencing the quality of their relationship, the history of these relationships is equally telling. Spike and Garth grew up with one another, were close in age and may even be related. Without the background history on Spike and Garth, a first-time observer to the Cafetal group would have no idea why these males spent so much of their time affiliating with one another. Diablo and Pirate, on the other hand, were at least 4 years apart in age, may not have come from the same natal group, and although their relationship was cooperative it was never highly affiliative. Pirate was also a small, unassertive male while Diablo was the center of the females' attention.

Are white-faced capuchins male-bonded?

The data presented in this study illustrates the variability in the social relations of male white-faced capuchins and demonstrates that some males do form close, enduring affiliative

relationships. But is this male-bonding? The answer is, yes, and no. Traditionally, the sex that is described as being bonded is the one that routinely forms enduring affiliative relationships. In white-faced capuchins, females fit this description. White-faced capuchins are considered female bonded (Wrangham 1980, 1987) or resident nepotistic (Sterck *et al.*, 1997) in that females are generally philopatric and males disperse, and bonds among females are generally stronger than those among males or between males and females. Female white-faced capuchins form enduring alliances, groom one another more than they groom males or males groom each other, and they are preferentially affiliative with members of their own sex (Perry, 1996a; Fedigan, 1993). The chimpanzee is the most oft cited example of a male-bonded species, and this bonding is evidenced by their high levels of grooming, sexual tolerance, alliance behaviour within groups, cooperative hunting, food sharing, and cooperation in intergroup aggression (van Hooff & van Schaik, 1994 and articles cited therein). Bondedness is often equated with "mutual tolerance and cooperation" (van Hooff & van Schaik, 1994) and male white-faced capuchins most definitely fit this description. They are the main participants in intergroup encounters and male cooperation is key in gaining access to a group and retaining membership in it. In fact, with the exception of high levels of grooming, cooperative hunting, and direct food sharing, male white-faced capuchins display all of the criterion of male-bonding observed among male chimpanzees.

It is important to keep in mind that even though white-faced capuchins are not routinely male-bonded, the data presented here demonstrates that they do have the capacity. The data collected on the white-faced capuchins of Santa Rosa are among the most detailed and complete of any New World species, and these represent a mere 17 years of data. Many species of Old World primates have been studied continuously since the 1950s and 1960s, and many changes in the way we conceptualize the behaviour of these primates have occurred over these decades. As our long-term research on white-faced capuchins continues in Santa Rosa, Lomas Barbudal and several other sites throughout Costa Rica, so too will our understanding of the conditions that lead to the bonding observed between males like Spike and Garth. Although it is inherently difficult to

monitor the movement of males through multiple migrations, this is a very important issue in the behavioral ecology of species characterized by male dispersal, and this information is absent for most primate species. This missing piece of the puzzle is necessary before any definitive conclusions regarding the quality of male relationships can be made.

Table 5.1 Independent variables for male dyads.

	Age Relationship	Group Size	Sex Ratio M:F	Rank Distance*	Relationship Length months
Diablo:Pirate LV	ad:ad	14	0.75	2	72
Diablo:Side LV	ad:ad	14	0.75	1	21
Side:Pirate LV	ad:ad	14	0.75	1	21
Leo:Regis BH	ad:sa	8	1	1	58
Leo:Casey BH	ad:sa	8	1	2	58
Leo:George BH	ad:sa	9	1.33	1	53
George:Regis BH	sa:sa	9	1.33	1	87
George:Casey BH	sa:sa	9	1.33	2	73
Regis:Casey BH	sa:sa	8	1	1	80
Spike:Garth CU	ad:ad	6	1	1	86
Nose:Trickle CP	ad:ad	9	0.5	1	25

LV = Los Valles group
BH = Bosque Humedo group
CU = Cuajiniquil group
CP = Cerco de Piedra group
ad = adult; sa=subadult
*Rank of subordinate dyad partner:rank of dominant dyad partner dominant

Table 5.2 Duration of male affiliative interactions (seconds/hour) with coresident adult females, adult males, and subadult males.

MALE group;age-class;rank hours observed	CONTACT Total Females Males	CONTACT REST Females Males	GROOM Females Males	PROXIMITY Total Females Males
DIABLO	385.87			237.99
LV;ad;1	303.70	178.60	114.72	151.33
49.25 hrs	1.20	0.00	0.77	1.02
SIDE	157.79			86.48
LV;ad;2	55.09	24.77	20.91	17.85
49.25 hrs	18.27	14.84	1.12	23.59
PIRATE	137.82			98.90
LV;ad;3	38.69	17.70	16.77	32.53
48.25 hrs	26.18	14.59	0.64	37.70
LEO	193.02			96.99
BH;ad;1	133.84	91.91	38.85	53.48
54.75 hrs	45.33	24.68	10.23	38.65
GEORGE	209.06			139.42
BH;sa;2	12.73	7.72	0.25	11.07
39.75 hrs	196.10	83.70	53.79	132.53
REGIS	413.42			105.86
BH;sa;2	247.50	204.70	28.05	70.94
52.75 hrs	169.04	82.60	17.38	45.00
CASEY	475.17			102.37
BH;sa;3	177.60	109.50	27.63	60.39
53.25 hrs	263.32	76.73	25.80	55.47
SPIKE	732.19			446.95
CU;ad;1	231.20	209.90	19.34	101.20
25.75 hrs.	481.09	440.16	20.58	349.71
GARTH	522.79			492.04
CU;ad;2	35.75	28.88	6.88	58.33
24 hrs.	485.96	452.68	26.50	435.29
NOSE	446.01			289.42
CP;ad;1	300.40	203.70	90.09	152.92
125 hrs	19.87	16.38	0.92	35.25
TRICKLE	215.59			169.05
CP;ad;2	70.44	44.62	14.83	28.62
120.25 hrs.	28.62	24.11	2.28	66.41
Mean/SE for all males	353.52/56.5 146.10/33.4 157.73/55.1	101.99/25.1 111.86/50.7	34.39/10.7 14.55/5.0	205.95/43.9 67.15/14.8 110.97/43.5
Wilcoxon signed ranks test	time in contact males vs. females: Z = -.178[a]; NS	time resting in contact males vs. females Z=-0.533[a], NS	time grooming males vs. females Z=-1.511[a], NS	time in proximity males vs. females: Z = -.622[b]; NS

a. based on positive ranks; b. based on negative ranks

Note: Regis' and Casey's rank were based on data after George emigrated

Table 5.3 Duration of male-male dyadic affiliative behaviors (seconds/hour).

MALE	CONTACT	CONTACT REST	GROOM	PROXIMITY
Diablo: Pirate LV; 97.5 hrs*	6.51	1.48	0.32	0.38
Diablo: Side LV; 98.5 hrs	3.95	3.31	0.39	4.31
Side:Pirate LV; 97.5 hrs	12.19	9.9	0.58	28.3
Leo:Regis BH; 107.5 hrs	19.53	6.82	1.3	26.69
Leo:Casey BH; 108 hrs.	27.22	13.3	7.75	10.61
Leo:George BH; 79.75 hrs	39.5	25	9.1	26.45
George:Regis BH; 81 hrs	73.06	40.2	16.81	51.7
George:Casey BH; 74.5 hrs	99.73	31.5	31.41	76.56
Regis:Casey BH; 106 hrs	195.12	111	17.93	34.6
Spike:Garth CU; 49.75 hrs	483.44	453	23.2	390.99
Nose:Trickle CP; 245.25 hrs	24.16	20.2	1.57	50.53
Mean for all males	89.49	65.00	10.03	63.74

*number of hours of focal data used in calculating rates combined hours for each dyad member
LV = Los Valles group
BH = Bosque Humedo group
CU = Cuajiniquil group
CP = Cerco de Piedra group

REFERENCES

Altmann, J. 1974. Observational study of behavior: Sampling methods. *Behav.*, 49:227-266.

Boinski, S. 1994. Affiliation patterns among male Costa Rican squirrel monkeys. *Behav.*, 130:191-209.

Fedigan, L.M. 1993. Sex differences and intersexual relations in adult white-faced capuchins *Cebus capucinus*. *Int. J. Primatol.*, 14:853-877.

Fedigan, L.M. & Baxter, M.J. 1984. Sex differences and social organization in free-ranging spider monkeys *Ateles geoffroyi*. *Primates*, 25:279- 294.

Fedigan, L.M., Rose, L.M. & Avila, R.M. 1996. See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In *Adaptive Radiations of Neotropical Primates*, (M. Norconk, A. Rosenberger & P. Garber, eds.). Plenum Press, New York, pp.289-308.

Fedigan, L.M. and Jack, K.M. in press 2001. Neotropical primates in a regenerating Costa Rican dry forest: A comparison of howler and capuchin population patterns. *Int. J. Primatol*, 22(5): 689-713.

Freese, C.H. 1978. The behavior of white-faced capuchins *Cebus capucinus* at a dry-season waterhole. *Primates*, 19:275-286.

Fragaszy, D., Fedigan, L.M. & Visalberghi, E. in prep. Social behavior: Interaction, relationships and social structure. In *The Complete Capuchin Monkey*. Cambridge University Press, Cambridge.

Goldberg, T.A. & Wrangham, R.W. 1997. Genetic correlates of social behavior in wild chimpanzees: evidence from mitochondrial DNA. *Anim. Behav.*, 54:559-570.

Goodall, J. 1965. Chimpanzees of the Gombe Stream Reserve. In *Primate Behavior*, (I. DeVore, ed.). Holt, Rinehart and Winston, New York, pp. 245-273.

Goodall, J. 1986. The chimpanzees of Gombe; Patterns of behavior. Harvard University Press, Cambridge.

Hill, D.A. 1994. Affiliative behaviour between adult males of the genus macaca. *Behav.*, 130:293 – 308.

van Hooff, J.A.R.A.M. 2000. Relationships among non-human primate males: a deductive framework. In *Primate Males: causes and consequences of variation in group composition*, (P.M. Kappeler, ed.). Cambridge University Press, Cambridge, pp.183-191.

van Hooff, J.A.R.A.M. & van Schaik, C.P. 1992. Cooperation in competition: the ecology of primate bonds. In *Coalitions and Alliance in Humans and Other Animals*, (S. Harcourt & F. de Waal, eds.). Oxford: Oxford University Press, Oxford, pp.356-390.

van Hooff, J.A.R.A.M. & van Schaik, C.P. 1994. Male bonds: affiliative relationships among nonhuman primate males. *Behav.*, 130:309-337.

Mitani, J.C., Merriwether, D. and C. Zhang. 2000. Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behav.*, 59:885-893.

Mitchell, C.L. 1989. *Resources, group behavior, and infant development in white-faced capuchin monkeys, Cebus capucinus*. PhD dissertation, University of California, Berkeley, University Microfilms International.

O'Brien, T.C. 1991. Female-male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. *Anim. Behav.*, 41:555-567.

Oppenheimer, J.R. 1968. *Behavior and ecology of the white-faced monkey, Cebus capucinus on Barro Colorado Island, Canal Zone.* PhD dissertation, University of Illinois-Urbana, University Microfilms International.

Pereira, M.E., Clutton-Brock, T.H. & Kappeler, P.M. 2000. Understanding male primates. In *Primate Males: causes and consequences of variation in group composition*, (P.M. Kappeler, ed.). Cambridge University Press, Cambridge, pp.271-277.

Perry, S. 1996a. Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Amer. J. Primatol.*, 40:167-182.

Perry, S. 1996b. Intergroup encounters in wild white-faced capuchin monkeys, *Cebus capucinus*. *Int. J. Primatol.*, 17:309-330.

Perry, S. 1998a. A case report of a male rank reversal in a group of wild white-faced capuchins *Cebus capucinus*. *Primates*, 39:51-70.

Perry, S. 1998b. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behav.*, 135:139-172.

Pusey, A. E. & Packer, C. 1987. Dispersal and philopatry. In *Primate Societies*, (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.). University of Chicago, Chicago, pp. 250-266.

Robinson, J.G. 1988. Demography and group structure in wedge-capped capuchin monkeys, *Cebus olivaceus*. *Behav.*, 104:202-232.

Rose, L.M. 1994a. Benefits and costs of resident males to females in white-faced capuchins *Cebus capucinus*. *Amer. J. Primatol.*, 32:235-248.

Rose, L.M. 1994b. Sex differences in diet and foraging behavior in white-faced capuchins *Cebus capucinus*. *Int. J. Primatol*,. 15:95-114.

Rose, L.M. 1998. *Behavioral ecology of white-faced capuchins Cebus capucinus in Costa Rica*. PhD dissertation, Washington University-St. Louis MI, University Microfilms International.

Rose, L.M. & Fedigan, L.M. 1995. Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Anim. Behav.*, 49:63-70.

Silk, J.B. 1994. Social relationships of male bonnet macaques: male bonding in a matrilineal society. *Behav.*, 130:271-291.

Sterck, E.H.M., Watts, D.P., and van Schaik, C.P. 1997. The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.*, 41:291-309.

Strier, K.B. 1994. Brotherhoods among atelins: Kinship, affiliation and competition. *Behav.*, 130(3-4):151-167.

Struhsaker, T.T. & Leland, L. 1987. Colobines: Infanticide by adult males. In *Primate Societies*, (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.). University of Chicago, Chicago:83-97.

Wrangham, R. 1980. An ecological model of female-bonded primate groups. *Behav.*, 75:262-299.

Wrangham, R. 1987. Evolution of social structure. In *Primate Societies*, (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.). University of Chicago, Chicago:282-296.

Zar, J.H. 1999. *Biostatistical Analysis*. Fourth Ed. Prentice-Hall Inc., New York.

CHAPTER SIX

General discussion and conclusions

When I began my study of male white-faced capuchins in Santa Rosa National Park (SRNP), my interests lay in determining why, given the social structure and dispersal patterns of this species, do these apparently unrelated immigrant males, residing together and competing for access to mates and resources, cooperate with one another? How are males benefiting by tolerating the presence of coresident males in their group? My first step towards answering these questions led to my examination of the dispersal patterns of this species. Throughout my 15 month field study of male white-faced capuchins in SRNP, I had observed several male migrations and I wanted to know how my observation compared to migrations previously reported for this species. I also wanted to know basic information about male dispersal, such as age at first emigration, frequency of parallel dispersal, and average tenure within groups. To obtain this information, most of which had not been previously published, I turned to the 17 years of behavioral and demographic observations collected on the white-faced capuchins of SRNP by Dr. Linda Fedigan and her students. My summary of this data base provides the first detailed account of male life history and dispersal patterns for capuchins.

What emerged from my compilation and summary of the data set was a portrait of a very transient monkey; one whose life is filled with changes, both physically and socially. Young male white-faced capuchins make their first move around the age of 4.5 years, and this sets the pace for many subsequent years of travel. The emigration of these males from their natal group is voluntary; males are either joining neighboring groups following intergroup interactions, or they are leaving their natal group in the company of dispersing group mates. Natal dispersal for this species, is not a solitary event. It appears to be motivated by an attraction to males, particularly to dispersing or previously dispersed group mates, as evidenced by the high rates of parallel dispersal in the Santa Rosa study population. The frequency of parallel dispersal observed among

male white-faced capuchins remained high even during secondary dispersal. Through the long-term observations by multiple researchers in SRNP, and the passing down of individual identifications, we have been able to document how one pair of males, most likely maternal siblings, dispersed together on three separate occasions.

Although secondary dispersal by male white-faced capuchins also often occurs in the company of familiar males, it appears to be in response to an attraction to extragroup mates. My finding that males were preferentially entering groups with more favorable sex ratios, is indicative of this attraction. Perhaps one of the most interesting findings from my summary of the long-term data from Santa Rosa, accompanied by my own observations of male transfer, was the opportunistic nature in which males move between groups. Unlike other species that tend to experience solitary periods between emigration and subsequent immigration (e.g. Japanese macaques: Sugiyama, 1976; mantled howlers: Glander, 1992; red howlers: Crockett & Pope, 1993), male white-faced capuchins are transferring directly into new groups. Solitary males, or small groups of 2-4 males, have been occasionally observed but they appear to be in the process of dispersing. I have followed several groups of these males, and on every occasion they have returned to a bisexual group by the end of the day. It appears as though these males are investigating their opportunities in neighboring groups. The Santa Rosa data base is filled with reports of males temporarily disappearing from the long-term study groups, usually only for a day or two, and these missing males are often spotted in the range of a neighboring group. In fact, the majority of emigrations documented for the Santa Rosa study groups are preceded by such reports. It seems that prior to completely disassociating themselves with their current group, males have secured residency, or at least investigated possible opportunities, within a new group.

My summary also demonstrated that the way in which males immigrate into new groups is dependent upon their age; immature and subadult males joined groups peacefully, taking up residence with males in the group, while adult males either moved into previously abandoned groups or aggressively entered a group, most often evicting resident males. It was interesting to

find that half of the aggressive takeovers documented over the past 17 years were enacted by single males, rather than cooperative alliances as has been previously stressed in the literature (e.g. Fedigan, 1993; Rose, 1994, 1998). All cases of single male takeovers involved target groups also containing a single adult male, and in the cooperative takeovers observed, the invading males always outnumbered resident males in the target group. This finding confirms the vulnerability that males face once they have lost the support of their coresident males and highlights the importance of male cooperation in maintaining group membership.

Male cooperation in defending the group from conspecifics enables males to retain membership in a group and thereby protects their access to mates (Rose & Fedigan, 1995). Part of this cooperation entails vigilance activities; that is, in order to best protect access to mates, males need to monitor their range for possible threats to their group. Therefore, males are also likely benefiting from the added protection garnered through the vigilance behavior of coresident males. Vigilance behavior has been previously used as an indication of the benefits that multiple coresident males provide one another, and has been hypothesized as a major factor influencing the evolution of multimale primate groups (e.g. van Schaik, 1983; van Schaik & van Hooff, 1983). Although it has often been assumed that male vigilance behavior is aimed at detecting predators, and thus assuring the safety of mates and offspring from the threats of predation (e.g. van Schaik & Höstermann, 1994), it has been demonstrated for *C. capucinus* that male vigilance is primarily directed at detecting extragroup conspecifics (Rose & Fedigan, 1995).

During the course of my study, one male emigrated from each of three study groups enabling me to test previous theories relating to the effect of multiple coresident males on male vigilance behavior. Specifically, I wanted to know what effect the emigration of a coresident male had on the vigilance behavior of males remaining in the social group. In my analysis I investigated two types of vigilance behavior: non-social vigilance (i.e., vigilance directed at detecting threats external to the group); and, social vigilance (i.e., vigilance directed at monitoring events occurring within the confines of the group). I compared rates of both types of vigilance for

periods before and after the emigration of a coresident male. The results of my analyses indicated that additional males within groups confer both costs and benefits to coresident males. Coresident males appear to be imposing costs on one another in that males need to devote more time to monitoring the social environment and my findings indicate that some males are monitoring the activities of their coresident males. Although not quite as conclusive as the results obtained on social vigilance, it does appear that some males benefit from the presence of multiple coresident males in that they are able to devote less time to non-social vigilance (vigilance directed at detecting predators and conspecifics). However, the vigilance behavior of males, particularly non-social vigilance, is highly variable and influenced by many factors (e.g. season).

Overall, the vigilance benefits that males gain by tolerating the presence of multiple coresident males seem minimal, particularly when the costs of time devoted to non-social vigilance are taken into account. This brings me back to my initial question of why these unrelated immigrant males cooperate with one another so reliably when it comes to intergroup aggression? The data on the frequency of parallel emigration reported in this study may be one of the primary reasons male cooperation is so prominent in white-faced capuchins. The frequency of young males disappearing together from their natal groups, accompanied by observations of males joining groups containing familiar males, indicates that co-resident males may in fact be related to one another. Male-bonding is expected to be more prominent in species containing related males, because under such circumstances the inclusive fitness benefits of tolerance and cooperation are expected to decrease within group mating competition (van Hooff & van Schaik, 1992). Recent studies have demonstrated, however, that kinship is not necessary for the formation of cooperative alliances (see van Hooff, 2000 and Strier, 1994). In the absence of relatedness between group males, familiarity can also be maintained through parallel dispersal and can be just as effective in promoting such cooperative alliances. The presence of known males within groups may also influence a male's choice of group. Therefore, regardless of whether or not coresident males are related, it is becoming increasingly apparent that many of the males we observe have

long histories together, and that these histories and male familiarity are influencing the nature of their relationships.

In the final data chapter I investigated male relationships within my four study groups. Although white-faced capuchins are generally considered female-bonded, my observations of several highly affiliative males during the course of my study, caused me to wonder what factors could be influencing relationships among males. Previous reports of male white-faced capuchins indicated that their relationships were extremely variable (e.g. compare Fedigan, 1993 with Perry, 1998), however, no one had ever compared male relationships between study groups. By comparing male intragroup relationships among my four study groups, I was able to take into account the following factors and test their effect on male relationships: group size, sex ratio, rank distance, and duration of relationship between males. This comparison of male relationships within my four study groups demonstrated that males residing in small groups, with fairly equal sex ratios, have a tendency to behave more affiliatively than those males residing in large groups with lower ratios of males to females. Male familiarity also had a significant effect on male affiliative relationships, and knowing the history between two males (e.g. rank history, personality) further helped in interpreting the results. Overall, male relationships are extremely variable in this species, much more variable than those observed among females or between males and females (see Perry, 1996, 1997), and although some males do form long-term affiliative bonds with one another, these are much less predictable than those observed among females.

The question of why male white-faced capuchins cooperate in group defense remains incompletely answered. It is possible that coresident males are related; dispersing natal males may be siblings (maternal or paternal), or more distantly related kin. The history between males in our study groups does seem to influence their intragroup interactions with one another; however, based on previous reports and my own observations, they do not appear to influence male participation during intergroup interactions. The benefits males are providing one another in

terms of vigilance behavior also seem too minor to guarantee male participation in group protection. It appears most likely that coresident males band together in protecting the group because they may all have something at stake. The relaxed mating system of this species indicates that all males have, or at least appear to have, reproductive potential within groups. During the course of my fieldwork all subadult and adult male members of my four study groups were observed mating on at least one occasion. However, it is possible that male mating competition within white-faced capuchins is occurring at the physiological level (i.e. sperm competition), or that females are preferentially mating with alpha males during times of conception. However, these questions will need to wait. Genetic and hormonal analyses have much to tell us.

Overall, the multimale groups of white-faced capuchins appear to have evolved out of necessity. Males, particularly adult males, need to cooperate in entering a group and maintaining residence within it. The male-biased infant sex ratio of the SRNP capuchins (Fedigan *et al.*, 1996), the near equal sex ratios within groups, and the ever increasing proportion of males within the park's population (Fedigan & Jack, in press), all work together to increase intragroup mate competition. As a result of this intense between group competition for mates, individual males are unable to monopolize access to female groups; there are just too many males to compete with (see Strier, 2000). Strier (1994) suggests that male reproductive strategies may reflect a compromise between inter and intragroup competition for access to females. This appears to be the case for male white-faced capuchins; between group competition for mates is more intense than within group competition and this, in turn, has lead to the cooperative group defense characteristic of this species. The high frequency of parallel dispersal likely works to maintain the multimale social structure of white-faced capuchins, and may have been an important factor influencing its evolution (see Strier, 2000).

Future research needs to continue monitoring known males through multiple transfers. This information is crucial to furthering our understanding of male life history patterns in this species. At the moment there is a large portion of this history that remains absent from our summary,

which ends with prime aged males. Additional data on older adult males, particularly the way in which they enter new groups, is necessary. Genetic analysis of male relationships and reproductive success are currently underway, and these results may help us to understand the diversity we observe not only in male relationships, but also in dispersal patterns.

REFERENCES

Crockett, C.M. & Pope, T.R. 1993. Consequences of sex difference in dispersal for juvenile red howler monkeys. In *Juvenile Primates*, (M.E. Pereira & L.A. Fairbanks, eds.). Oxford University Press, New York, pp. 104-118.

Fedigan, L.M. 1993. Sex differences and intersexual relations in adult white-faced capuchins *Cebus capucinus*. *Int. J. Primatol.*, 14:853-877.

Fedigan, L.M., Rose, L.M. & Avila, R.M. 1996. See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In *Adaptive Radiations of Neotropical Primates*, (M. Norconk, A. Rosenberger & P. Garber, eds.). Plenum Press, New York, pp.289-308.

Fedigan, L.M. and Jack, K.M. in press 2001. Neotropical primates in a regenerating Costa Rican dry forest: A comparison of howler and capuchin population patterns. *Int. J. Primatol*, 22(5): 689-713.

Glander, K.E. 1992. Dispersal patterns in Costa Rican mantled howler monkeys. *Int. J. Primatol.*, 13:415-436.

van Hooff, J.A.R.A.M. & van Schaik, C.P. 1992. Cooperation in competition: the ecology of primate bonds. *Coalitions and Alliance in Humans and Other Animals*, (S. Harcourt & F. de Waal, eds.). Oxford University Press, Oxford.

van Hooff, J.A.R.A.M. 2000. Relationships among non-human primate males: a deductive framework. In: *Primate Males: causes and consequences of variation in group composition*, (P.M. Kappeler, ed.) Cambridge University Press, Cambridge, pp.183-191.

Perry, S.E. 1996. Intergroup encounters in wild white-faced capuchin monkeys, *Cebus capucinus*. *Int. J. Primatol.*, 17: 309-330.

Perry, S.E. 1997. Male-female social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behav.*, 134:477-510.

Perry, S.E. 1998. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behav.*, 135: 139-172.

Rose, L.M. 1994. Benefits and costs of resident males to females in white-faced capuchins *Cebus capucinus*. *Amer. J. Primatol.*, 32:235-248.

Rose, L.M. 1998. *Behavioral ecology of white-faced capuchins Cebus capucinus in Costa Rica*. PhD dissertation, Washington University-St. Louis MI, University Microfilms International.

Rose, L.M. & Fedigan, L.M. 1995. Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Anim. Behav.*, 49:63-70.

van Schaik, C.P. 1983. Why are diurnal primates living in groups? *Behav.*, 87: 120-144.

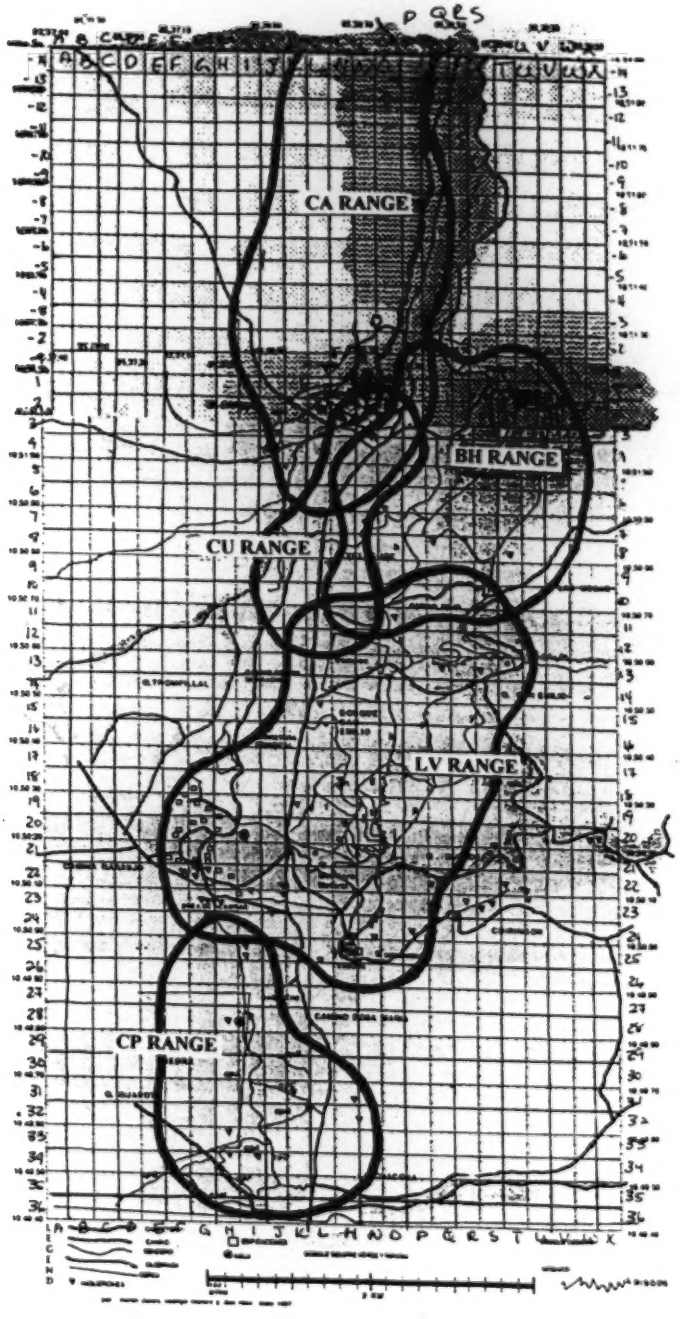
van Schaik, C.P., and van Hooff, J.A.R.A.M. 1983. On the ultimate causes of primate social systems. *Behav.*, 85: 91-117.

van Schaik, C.P., and Höstermann, M. 1994. Predation risk and the number of adult males in a primate group: a comparative test. *Behav. Ecol. Sociobiol.*, 3: 261-272.

Strier, K.B. 1994. Myth of the typical primate. *Yrbk. Phys. Anth.*, 37:233-271.

Strier, K.B. 2000. From binding brotherhoods to short-term sovereignty: the dilemma of male Cebidae. In: *Primate Males: causes and consequences of variation in group composition*, (P.M. Kappeler, ed.) Cambridge University Press, Cambridge, pp. 72-83.

Sugiyama, Y. 1976. Life history of male Japanese monkeys. In: *Advances in the Study of Behavior, Vol. 7* (Rosenblatt, J.S. ed.) Academic Press, New York, pp.255-284.

APPENDIX A

Group home ranges